THE USE OF SPIDER SILK IN THE NESTS OF SMALL BIRDS, WITH PARTICULAR REFERENCE TO THE CHAFFINCH (*FRINGILLA COELEBS*).

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by

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SUMMARY

A very wide range of smaller passerine birds employ silk, from spiders and other arthropods, as a nesting material. The nest is an important feature of bird breeding behaviour, success being dependent in part upon the structure of the nest and the timing of construction of the nest. Spiders can spin many different types of silk, with varying properties, but all spider silks are remarkably strong and extensible. In addition, web silk is adhesive and represents a renewable resource. This study has shown that the chaffinch uses spider web and cocoon silk. Cocoon silk attaches lichen to the outside of the nest, and holds together the moss structure. Web silk is used in more general roles, and usually to a lesser extent; it appears to be an all purpose bonding material, attaching a range of materials to the outside of the nest, and binding together other structural materials. Web silk is also used to attach the nest to the twigs of the bush or tree in which it is built.

Using scanning electron microscopy, it has not been possible to identify with any certainty the spider families which spin the cocoon silk used, but all web silk found in chaffinch nests appears to belong to the family Amaurobiidae. These webs are spun flat against rough tree bark and on fences *etc.*, and trap insects by entangling them in extremely fine fibrils. The amount of this silk present at Garscube Estate, on the edge of Glasgow, starts to rise just before the onset of chaffinch nest building. It is proposed that nest-building is not restricted in location by the availability of this common silk-type, but the birds may be prevented from building earlier in the season by a lack of these webs in the environment. However, the use of silk appears to enable them to breed in areas where the sites and materials available for nest-building are not ideal.

It may be possible to generalise these findings for the chaffinch to other temperate, and tropical, passerines that employ silk as a nesting material. Compared with chaffinch nests, the extent of silk usage can be far greater, and the number of functions it fulfils far wider,

in nests of other birds. The birds may consequently find themselves more restricted in time and place of breeding where the types of silk needed are not in abundance.

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CHAPTER 1

INTRODUCTION

Silk produced by spiders and other arthropods appears to be widely used by birds as a nesting material. In common with other aspects of nest architecture, silk use has been poorly treated in the literature. There is little information on the families that use silk, and reasons why some families use it extensively, and others not at all.

Silk use does appear to be restricted to the order Passeriformes, and among those, the smaller birds tend to be more likely to employ silk in their nests. Hansell (1984) lists 23 passerine families known to use silk as a nesting material. This is a minimum picture of an extremely widespread phenomenon. Only 19 works on birds nests are cited by Hansell.

However, none of these works gives much, if any, information about what types of silk are used, where the silk comes from, where the silk is placed in the nests, and what is achieved by using silk. A typical entry in one of these references would state that green spider cocoons are used as decoration (*e.g.* North 1904, on monarch flycatchers). Silk is apparently an extremely important nesting material, judging by its widespread use, and abundance in many nest types.

One trend that is noticeable is that those nests that typically contain silk are described subjectively as being tidier, neater or more compact than nests that are similar in structure but do not contain silk. As a general rule, larger birds build platforms of twigs as nests, but smaller birds often make nests from a more or less heterogeneous mass of plant materials, using silk to fasten together various materials and to attach the nest to the supporting vegetation (Collias 1964).

Collias (1986), in a brief survey of the relationship of nest structure to environment, says that silk is often a component of cold-adapted nests, but is not mentioned in adaptations to nests in hot or dry environments, nor as an adaptation to wind and rain.

Important information that have not been offered in these works includes what types of silk are involved and where they come from, what the extent of silk usage in each nest is, whether all nests of the same species use silk to the same extent, and what purpose does the silk serve in the nest.

A cursory look at a variety of nests revealed to me considerable variation in the extent of silk use. The nests of most fantails of the family Muscicapidae are constructed from a woven meshwork of grasses, the whole covered in a thin, even layer of silk. The main structure of the long-tailed tit (*Aegithalos caudatus*) nest contains an enormous amount of silk, creating a highly flexible structure. At the other extreme, the blackcap *Sylvia atricapilla*, builds a nest of woody fibre, with only occasional fragments of silk, possibly to reinforce the structure.

Various other possible roles of silk in birds nests have been proposed. For example, the Indian tailor bird uses silk to stitch together large leaf fronds to form a cup in which the nest is built. Hummingbirds use sticky silk to bind their nests to hanging leaves, where they are protected from the elements and inaccessible to predators.

Silk can be used to tie the nest to twigs or reeds *etc*, as in some honey-eaters (Meliphagidae) and orioles (Oriolidae and Icteridae). In the white-eyes, (*Zosterops* spp), the only attachment to supporting twigs is with silk. Tailor birds, of the genus *Orthotomus* in Asia, and genus *Cisticola* in Africa (both family Sylviidae) stitch leaves together using silk, thus forming the outer envelope of the nest (Hansell 1984).In a similar manner, spiderhunters (family Nectarinidae, subfamily Arachnotherinae) bind vegetation together

using rivets of silk punched through leaves (Hansell 1984).

Pendulous nests are often attached with silk to the overhanging vegetation. Sometimes, silk is the only material in this attachment. For instance the nest of the rock warbler (*Origma solitaria*) has an attachment made almost entirely from cobwebs (Collias 1986). Many hummingbirds from the tropics attach their cup-shaped nests to drooping living leaves, which act as a roof, frequently using silk (*e.g.* Skutch 1973).

Silk, primarily in the form of spider cocoon, can also form a decorative or camouflaging outer layer. In *Terpsiphone* this outer layer is exclusively made from papery sheets of silk, spun by the spider to cover its eggs. In other birds, such as some honeyeaters, such silk is mixed with lichens in the outer layer.

All too often in accounts of bird nests, the silk content is not considered. It is even unknown in most cases whether the silk is from spiders at all, other arthropods, such as moth larvae (like the silk worm *Bombyx mori*) can also produce large amounts of silk. We can not assume that where a nest description includes 'cobweb' that the author has in any way confirmed that the silk is really from spiders. However, it is rare that an account will describe the silk present as from any other arthropod.

Some of the more familiar British species that use silk include the blue tit (*Parus caeruleus*, family Paridae), the long-tailed tit (*Aegithalos caudatus*, family Aegithalidae), whose nest structure is composed of a very high proportion of silk, the goldcrest (*Regulus regulus*, family Phylloscopidae), and the chaffinch (*Fringilla coelebs*, family Fringillidae). The last named is the species that will be studied in the thesis, because of its abundance, its ability to breed in a wide range of habitats, its nests being distinctive but showing large variation in detail, and Chaffinches are known to use silk in their nests.

So this study is aimed at investigating the phenomenon in rather more detail, and

providing some clues as to why all members of some species use silk, while only some nests of other species use silk, but the rest do not.

Unanswered questions that will be looked at in this study are :

1) What are the properties of spider silk and silken structures that make it such a widespread nesting material?

2) What are the possible roles of silk in the nest?

3) What types of silk are used?

4) Could nesting be limited in time or space by silk availability?

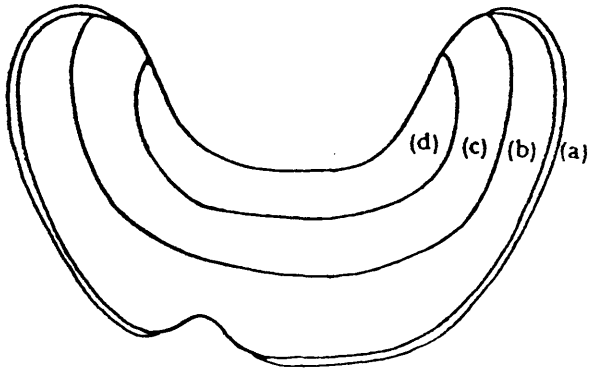

Figure 2.1 Vertical section of a typical chaffinch nest, from Marler (1956). Layers are (a) the superficial layer, (b) the foundation, (c) the inner layer, and (d) the lining.

CHAPTER 2

CHAFFINCH BREEDING BIOLOGY

2.1) THE STRUCTURE OF CHAFFINCH NESTS

Chaffinch nests can be found in many different situations. Trees and bushes are the most common localities, with deciduous trees favoured over conifers, and occasionally, nests have been found on fences (Tomek and Waligora 1976). Normally they are placed on the fork of a branch, almost never hanging by the rim (although one nest found in the current study was tied to branches with spider silk at the rim).

A generalised structure and composition of a typical chaffinch nest has been proposed by Marler (1956), based on the structure of two nests described in detail by Van Dobben (1949), and shown in figure 2.1. Four layers are distinguished by these authors. From the inside outwards they are: the Lining; the Inner Layer, including the rim; the main Foundation; and the Superficial covering. The findings of van Dobben (1949) and Marler (1956) can be summarised as follows. The cup is lined with a wide range of materials including roots, feathers, hair, wool, fur and moss setae. It is woven, but contains no spiders' silk. The inner layer and rim are composed of fine moss fragments, thin roots, and dry grass. Silk is not used to hold this layer together. The main foundation is a cup primarily of moss with some grass, usually knitted together with arthropod silk, although Van Dobben is not certain of the presence of cobwebs. This foundation is built around the supporting twigs, and/or tied to them with cobwebs. Spiders' webs are also used as a base adhesive in the first stage of construction, when the female may be taking nesting material to more than one potential site (Voipio 1988). The superficial covering, where present, is

composed mostly of lichen and silk cocoons of arthropods. Again, Van Dobben could not identify cobwebs with any certainty in this part of the nest.

Variations on this structure, and in the types of materials used, depend upon availability of materials in the territory, and the location of the nest (Marler 1956). In an examination of 57 nests from Poland, Tomek and Waligora (1976) found 22 different materials. Generally in the finches, the more concealed a nest is, the less tidy it is (Newton 1972), and for chaffinches Van Dobben (1949) suggests a correlation between the degree of exposure and the elaboration of external decoration with lichen and web. Furthermore, Marler's (1956) close observations of the behaviour of breeding pairs showed that nest material appears to be collected from a range of locations within the territory, even if there is more than sufficient in just one location.

2.2) THE CONSTRUCTION OF NESTS BY CHAFFINCHES

The nest is constructed in 3 stages - the foundation layer is built first, followed by the inner layer, and finally the lining and the superficial layer are added (Marler 1956). Different materials are used at different stages. According to Marler (1956), silk from spider webs, and some spun by other groups of arthropod, predominate together with moss in the early stages, but are collected less as the nest nears completion. This early period coincides with the construction of the foundation moss layer. The last stage, where the superficial covering is constructed, does not show a corresponding rise in the frequency of silk collection, or of lichen collection, so the truth may be that materials for this layer can be brought at any stage, and the layer constructed all through the nest-building phase. Indeed, Marler (1956) contradicts himself in saying that the superficial layer is constructed last, but lichen can be collected at any point in the process. Roots, feathers, and other materials which tend to make up the majority of the lining, are collected more than the other materials at the final stages of construction.

Where a second nest is built in the same season, either due to failure of the first or in an attempt to produce a second successful brood, materials from the first nest are frequently used. Hamel (1943) studied several pairs, and in no case was a second nest built without using materials from the first. Barret (1947), in an account of one breeding pair in Germany, watched a second, third and fourth nest being built, each reusing materials from the previous one. Only the second nest was successful, and the male fed this brood alone, while the female built the later nests after the young had fledged.

2.3) CHAFFINCH TERRITORIES

Territory sizes in Britain vary very much between habitat-types. They are smallest in dense, mature deciduous woodland, with an average size of 6,000 m^2 (145 pairs/Km^2), and largest in pine woods at 34,500 m^2 (30 pairs/Km^2) (Newton 1972). Small territories indicate a high degree of competition in deciduous wood (Newton 1972), or a habitat where supplies are plentiful, and hence competition is low. Territories can also be found in hedgerows in farmland, as well as well-timbered parks and gardens, such as Garscube Estate, where the number of pairs can be as dense as in the best woodlands. This wide range of suitable habitats, as well as a varied diet consisting of many types of seed and invertebrates, has contributed to the chaffinch being the most common woodland bird in Europe, with a geographical range from the most northerly European woodlands to as far south as north Africa, and as far east as Iran and Siberia.

2.4) THE TIMING OF CHAFFINCH BREEDING SEASONS

In order to assess how much silk is available for use in chaffinch nests, and how the

birds may be able to adapt to this, we need to know the timing of chaffinch breeding, and how it is thought to be controlled, both causally and functionally.

Data for the timing of events in the breeding cycle comes mostly from Marler's (1956) study on chaffinch populations around Madingley, near Cambridge, England. Further north, where the onset of spring occurs later, breeding tends to be delayed (Newton 1964).

The onset of physiological changes in preparation for the breeding season starts as early as January in British finches, in response to changes in daylength (Newton 1972). Steady enlargement of the gonads is accompanied in the male by changes in colouration from the dull winter plumage to the striking spring plumage. The first behavioural indication of the onset of the breeding season is the return to breeding areas in migratory races, and the establishment of territories by males (Marler 1956). Older males move into the same territory they held the previous year, towards the end of February, and first-year males start to attempt to set up territories about one week later.

A few days after the male has come into full song, while establishing territory boundaries, the females arrive, apparently attracted by the loud singing (Newton 1972). After around six weeks courting, and particularly during a mild weather, the female starts examining potential nest sites. This usually occurs around mid-April, after which, when she has made her selection, nest-building starts. This takes an average of 7 days (Newton 1972). Experienced birds, building a second nest from the materials of an abandoned first nest can take just 3 days. In contrast, young inexperienced females can take up to 18 days to build a nest, bringing materials in the wrong proportions, or in the wrong order, for rapid nest-building (Marler 1956). Around this time, the male may attempt copulation, but is unsuccessful unless solicited by the female. Copulations continue until the female starts incubating after laying the penultimate egg. Most clutches in the south of Britain are started in late April or early May, each female laying between four and six eggs on successive days (Newton 1972). Nest building can continue into the egg-laying period, until

incubation starts. Eggs hatch after 9-16 days of incubation (Newton 1964), and nestlings are fed mostly on defoliating caterpillars. In common with other birds, timing of breeding in the chaffinch is designed so that the nestling phase starts as the numbers of these prey items start to peak (Newton 1972).

Most young leave the nest on the 13th or 14th day, but remain well concealed in dense vegetation, and continue to depend upon their parents for food until they are over 30 days old. So by late June or early July, the parent chaffinches are freed from looking after their young, and the breeding season is complete (Newton 1972).

Rarely, early breeders who are successful may attempt a second clutch, either in the same nest as the first clutch (Newton 1964), or in a new nest built a few days after the first young have fledged (Barrett 1947). In these cases, the male takes over the care of the first brood, while the female incubates the second. Pairs whose broods have failed either as eggs or nestlings may attempt one or more repeat clutches, thus delaying completion of the cycle. Therefore it is possible for nest construction to continue into early June. Whether timing of breeding is adjusted to coincide with optimum availability of nesting materials, specifically spider silk since it appears to be the material that limits the speed of construction, is unclear. Part of this study will examine how silk availability varies through the year.

2.4.1) Geographical variation in the timing of breeding

Birds breeding in Scotland start on average a fortnight later than those in south-west England, and 10 days later than those in the north of England, according to Newton (1964) who compiled data from over 3,500 nests records over a 24 year period between 1934 and 1960. This can be attributed to the later start of spring in higher latitudes, where the peak in insect-prey numbers appears later. It could be possible that a different set of

cues are used at different latitudes to determine the timing of breeding so that success is optimised.

2.5) TIME AND ENERGY BUDGETS OF CHAFFINCHES DURING THE BREEDING PERIOD

Studies were carried out by the Zoological Institute of Leningrad on a population of chaffinches, using observations on both wild and captive birds in northern Europe. They monitored more than 2000 nests from 1000 adults, which were breeding at a density of 218 pairs per km^2, between 1958 and 1977 (Dolnik and Payevsky 1982). It was a migratory population, spending winter in southern France and the south-west of the Iberian Peninsula (Lyuleeva 1982).

On average, males spent 4.8 hours each day in reproductive and related behaviour (including territorial defence, courting, maintenance of the female on the nest and feeding the young) over the whole breeding season, while the females spend 8.3 hours per day (courtship, nest-building and daytime incubation and brooding, and feeding young, but excluding nighttime incubation and brooding (Ilynia 1982)). The average duration of nest-building was 5.12 days (Ilynia 1982), 2 days shorter than Marler's (1956) study in southern England. Family groups remained together for a mean of 29 days (Ilynia 1982), again less than in southern England.

Energetic costs were calculated for nest-building (0.72 Kcal/day or 11.6 Kcal/nest), egg formation (3.34 Kcal per egg weighing 2.2g) and incubation (2.6 Kcal/day). These make up a total of one third of the total daily metabolic energy of the female chaffinch (Dolnik 1982). For a pair, 18% of total productive energy is devoted to nest-building, egg formation and incubation, 25% to nestling feeding, 28% to territory defence, and 29% to other sexual behaviours (Dolnik and Ilynia 1982).

This gives a picture of the enormous amount of time and energy put into breeding as part of a chaffinch's daily energy expenditure. If that input is not to be wasted then each stage has to be successful. In particular, the nest must be designed and constructed as economically as possible, and to the best of the female's ability, given the limitations imposed upon her by the materials she can use, and the ways she can manipulate those materials. All subsequent breeding effort, in terms of time and energy, in that season will be wasted if the nest has not been built to withstand the various environmental pressures to which it may be subjected.

2.6) REASONS FOR NEST ABANDONMENT BY CHAFFINCHES

Given the high energetic and temporal costs of nest-building and incubation, why is there a high incidence of nest abandonment? Newton (1964) gives figures showing that only 44% of chaffinch clutches produce one or more fledglings, and the number of nests started but abandoned before egg-laying, though unrecorded, is high (Marler 1956).

Reasons for abandoning before laying are unclear. Severe weather increases the chances of desertion, and strong winds may partly dislodge a nest (Marler 1956). Marler also suggests that desertion may be a way of delaying the timing of breeding if the weather turns adverse for long enough to delay the peak in insect prey numbers. Desertion can also be caused by human interference, death of one of the breeding adults, or the laying of an infertile clutch. The latter appears only to be ascertained by the female if hatching has not occurred after the 'normal' incubation period (Newton 1964). Finally, nest predation accounts for nearly 70% of nest failures (Newton 1964). Magpies (*Pica pica*) make up over half observed predations, locating the nest by watching the parents during the nestling phase. Other predators, suspected and observed, include jays (*Garrulus*

glandarius), grey squirrels (*Sciurus carolinensis*), stoats and weasels (Newton 1964).

In this study, where nests from the study area need to be collected, the number that may be found in good condition will be influenced by the incidence of nest abandonment. Large predators will generally destroy the nest, but successful nests too will be damaged or disturbed by the activities of the nestlings within it. Those nests abandoned during building probably will not contain as much information for the purposes of this study as complete nests. On the whole, the nests in best condition will provide the greatest amount of information - that is those predated during the brooding or early nestling phases, and those abandoned after completion. Nests found in less than perfect condition could give indications as to what designs of nests are most efficacious.

2.7) THE IMPORTANCE OF THE NEST TO BREEDING SUCCESS

The whole success of a chaffinch pair's reproductive effort depends upon constructing a nest that is strong, insulating, and concealed from potential predators. Such a nest must be constructed from the materials available in the territory at the time of nest building. It can be imagined that time spent on collecting one type of material will depend both upon availability of that material, and upon its importance in the nest relative to other suitable materials.

There is evidence which suggests that it is silk that appears to be the limiting material in the speed of nest construction. Marler (1956) attributes the longest nest-building phase of young females, to be not due to lack of 'motivation', but rather to the number of cobwebs collected. He observed the youngest females, which took up to eighteen days to build a nest, collecting a far greater proportion of webs than more experienced females. Whether this is because more webs are needed in a nest built by an inexperienced female, or whether they are surplus to requirements is not speculated upon by Marler. In accord with

the speed limitations imposed by web collection, Marler (1956) claims that the rapid building of second nests is facilitated by reusing the webs of the old nest, "which normally take much time to collect". Hence, it should follow that silk is one of the most important elements of the nest.

On the other hand, as we shall see, and as van Dobben has indicated, silk is not used in all chaffinch nests by any means. My study aims to assess precisely the role of silk in chaffinch nests, and how timing of breeding may be affected by silk availability, or how silk availability may control the length of the nest-building phase. It may be valid to generalise these ideas and apply them to other small birds that use silk in their nests.

CHAPTER 3

SPIDERS AND THEIR SILK

3.1) SPIDER CLASSIFICATION

World-wide, there are estimated to be over 30,000 species of spider in 60 families (Foelix 1982). A simple classification of families found in Britain, as currently accepted would be as in table 3.1.

This classification is keenly disputed, particularly regarding the grouping of Cribellata as an infraorder. It has been argued (e.g. Coddington 1986) that the cribellum, the distinguishing feature, arose more than once in evolution, and that the orb web is of monophyletic origin. This would place the Uloboridae in the same group as the Araneoidae. Eberhard (1982) presents strong arguments for a classification close to that given in table 3.1., where the orb web evolved more than once, and the cribellum is monophyletic.

The natural history of the larger families has been reviewed by Foelix (1982), Jones (1983) and Preston-Mafham & Preston-Mafham (1984). The following overview, presented so as to familiarise the reader with the families, is based on these works. Later, I shall discuss how the natural history can affect the availability of silk to birds (see section 3.5).

ECRIBELLATAE

This group is distinguished by possessing no silk-spinning plate, the cribellum,

Table 3.1 A classification of the major British families of spiders, as generally accepted. Included are other families, important from the point of view that studies have been carried out on them, which are are mentioned in the text. Based on Foelix (1982) and Jones (1983).

Order ARANEAE

Suborder Orthognatha (Mygalomorphae)

Family Atypidae

Suborder Labidognatha (Araneomorphae)

Infraorder Ecribellatae

Family Scyotidae
Oonopidae
Dysderidae
Segestridae
Pholcidae
Gnaphosidae
Clubionidae
Liocranidae
Zoridae
Anyphaenidae
Sparassidae
Thomisidae
Philodromidae
Salticidae
Lycosidae
Pisauridae
Agelenidae
Hahnidae
Mimetidae
Theridiidae
Tetragnathidae
Metidae
Araneidae
Linyphiidae

Infraorder Cribellata

Family Eresidae
Amaurobiidae
Dictynidae
Uloboridae
Filistatidae

characteristic of the cribellates, though some families do show a vestigial ridge, the colulus, in its place. The only silk-spinning organs are the four or six spinnerets at the tip of the abdomen.

LYCOSIDAE

These are mainly ground-hunting 'wolf' spiders, found in fields and gardens, hunting by sight and by tactile stimuli. The female attaches her lens-shaped cocoon to her spinnerets and carries it with her until the spiderlings emerge. The family can be found in a wide range of open habitats

AGELENIDAE

These spiders build a flat sheet web of densely spun dry silk, amongst rocks and vegetation, with a tubular retreat, where the occupier lies in wait until an insect falls onto the sheet. The family includes the house spider *Tegenaria*. Other typical habitats include low vegetation and under stones in most areas.

THERIDIIDAE

Sometimes called the 'widow spiders', these are small spiders that build irregular scaffolding webs. In some, the web forms a loose sheet, under which are spun the mooring lines. These threads are studded with sticky droplets and break easily to trap any crawling insect which touches them. Other members of the family do not create a loose sheet, rather an irregular 3-dimensional structure, whose outermost threads are viscid. The family is found in a wide range of habitats including foliage of trees, low vegetation, under stones and around houses.

ARANEIDAE, METIDAE, TETRAGNATHIDAE

These are the familiar builders of the sticky orb web, and include the subject of many studies, the garden, or cross spider, *Araneus diadematus*. Spiders of these families either sit in the centre of the web or in a retreat connected by a signal thread to the centre,

waiting for prey to strike the viscid capture threads. The spiders are found in all habitats from lowlands to mountains, open grassland to damp caves, and from fences to low vegetation and trees of all species.

LINYPHIIDAE

This is the largest family in Britain, and popularly known as money spiders. They build sheet webs, under which the spider hangs until an insect strikes the scaffolding threads above the sheet and fall onto the sheet. The spider pulls its prey through the web, later repairing the hole. The silk in the sheet is probably slightly viscid, but the coating usually does not gather into globules (Gertsch 1949, Peters 1987) as it does in the Araneidae and Theridiidae. The spiders are typically found in low vegetation.

CRIBELLATA

This group of spiders is distinguished from the ecribellates by the presence of an extra silk-spinning apparatus, the cribellum, which is a plate positioned immediately anterior to the main spinnerets. It is associated with a comb-like array of teeth situated on the fourth metatarsus (the penultimate segment of the most posterior leg), called the calamistrum. Although Marples (1962) describes the product of the cribellum as a jelly-like material which is scollopped by the calamistrum, it is now certain that it is a very fine silk, combed out by the teeth of the calamistrum, and gathered into woolly bundles, termed "puffs". This silk forms the distinctive hackle-band, or cribellar capture thread (Peters 1987), that is the hallmark of the group, trapping insects by entangling any rough surface. Savory (1952) described the hackle-band as an unsurpassed material for entangling a struggling insect.

AMAUROBIIDAE

These nocturnal spiders produce the funnel webs in wall crevices and on tree bark. The cribellate silk gives the web a distinctive bluish appearance when fresh. The spider waits in

its retreat, under a stone or under bark, for a crawling insect to touch the web and become entangled.

ULOBORIDAE

Although only two species are present in Britain (*Uloborus walckenarius* Latrielle and *Hyptiotes paradoxus* (C.L. Koch)) and both are very rare and absent form Scotland, the family has been the centre of much attention due to the orb web they spin. The design is very similar to that of the Araneidae, but rather than having a viscid spiral, cribellate silk forms the catching thread. The similarity of the web extends to the method of its construction, leading many to conclude that it is closely related to the Araneidae. It is around this argument that most of the debate about spider phylogeny is centred.

3.2) SPIDER SILK PRODUCTION

A filament external to the animal, produced from a protein solution secreted in special glands in an arthropod is termed a silk (Lucas *et al.* 1960). The viscous liquid in the glands is drawn through a fine orifice, and this pulling action causes the molecules to become arranged as a fibre. This definition does not specify a precise chemical composition, nor does it describe any physical properties (Denny 1980), both being highly variable from one silk to the next.

Silk is produced by many groups classified as arthropods. Among the insects, the orders Coleoptera, Dictyoptera, Diptera, Embioptera, Hymenoptera, Lepidoptera, Neuroptera, Aphaniptera, and Trichoptera all produce silk at some stage of their life cycle (Lucas & Rudall 1968, Kenchington 1984). Chilopods, Diplopods and Pauropods produce silk mainly for use in sperm-transfer (Kenchington 1984). The arachnid orders Pseudoscorpiones and Acarinae produce silk for a variety of purposes, but the greatest

distribution and variety of silk production is found in the Araneae. All the families produce silk for various purposes such as prey capture, prey swathing, nests, cocoons (or egg sacs), retreats, and in courtship and mating. Kaston (1964) lists 15 uses across the families. These are given in table 3.2. One-dimensional linear constructions will be of little use to birds as a nesting material, as generally will the smaller of the two- and three-dimensional structures such as the sperm web or bridal veil, which in any case are only temporary. However the properties of some small structures, such as attachment discs, could be exploited by birds where they are produced in association with the larger structures that contain more silk. Of these the structures most evident in the environment, and most likely to be used in nests, are the webs, cocoons and retreats. The web is the device that traps spiders' prey. The cocoon is the structure in which eggs are laid and protected and where the young spiderlings undergo their first moult before emerging. The retreat is constructed by the spider to hide itself when in danger, to protect itself from the elements, or to wait until an insect strikes the web. It is with these three silken structures being used as nesting materials that this project is chiefly concerned.

3.2.1 Silk glands and the different types of silk

Several different types of silk can be produced by an individual spider. Each silk has a specific purpose, and is produced by a separate gland or set of glands. Each of the silk types has a different amino-acid sequence, which confers upon it its own unique physical properties (e.g. De Wilde 1943, Lucas 1964, Peakall 1964, Denny 1976, and see section 3.4). The birds that use silk in their nests may be able to distinguish between silk types, and thus exploit the different properties of each. The basis upon which a bird could make this distinction could be the appearance of the silk (for instance, silk from different glands can be of different colours), or the spider-spun artefact in which it is found.

Each individual gland has its own duct which opens to the outside *via* a spigot (a tiny collar-shaped chitinous opening), situated on one of the spinnerets. These are located just

Table 3.2 The useage of silk by spiders. Three categories are shown, according to the number of dimensions they occupy, under which are listed the various silken structures produced by spiders (after Kaston 1964).

I Linear constructions
- a) Draglines, continuously spun as the spider moves
- b) 'Parachute' gossamer threads

II 2-dimensional structures
- a) Attachment discs, attaching the dragline to the substrate
- b) Swathing band around prey
- c) Tie band of certain hunting species
- d) Hackle band of cribellates (catching thread)
- e) Sperm web
- f) 'Bridal veil' that a male uses to hold down a female

III 3-dimensional structures
- a) Web
- b) Cocoon
- c) Retreat
- d) Hibernating chamber
- e) Moulting chamber
- f) Mating chamber
- g) Nursery for spiderlings

anterior to the anal tubercle, at the tip of the abdomen. Certain types of gland appear in paired groups, but others exist only as a single pair.

The number of gland types differs from family to family, according to their life-styles and ecology. For example, members of the Lycosidae (wolf spiders), which actively hunt prey, have up to five types (Richter 1970), whereas those of the Uloboridae, the cribellate orb weavers, have up to 9 (Kovoor and Peters 1988).

The best studied families are the ecribellate orb-web spinning Araneidae (Epeiridae or Argiopidae in older works) and the Uloboridae. The *Araneus* genus has received most attention, particularly the garden spider *A. diadematus* Clerck. The glands have been named according to their morphology: ampullate, piriform, aciniform, tubuliform (or cylindrical), flagelliform (or coronate) and aggregate. The cribellate spiders have, in addition, cribellar and paracribellar glands, but lack the aggregate glands. This system can be further subdivided on the basis of size. For instance, it is generally agreed that araneids possess a pair of major and a pair of minor ampullates, which are of similar morphology but different size.

The types of silk that are distinguished in the Araneidae are the swathing bands used to wrap prey, the drag-line (the safety line spun behind the spider as it moves), the frame and scaffolding of the orb-web, the radii of the orb-web, the core and viscid coating of the catching spiral, the attachment disc which fastens the frame and dragline to the substrate, and cocoon silk. The plan of an orb-web, applicable to both araneids and uloborids, is shown in figure 3.1. As we have seen in table 3.2, the range of uses of silk is much wider than those mentioned above, so some glands must contribute silk to more than one structure.

Relating the silk to the gland that produces it has proven to be far from simple. Some workers have watched which spinneret is used, and then dissected the spider to see which

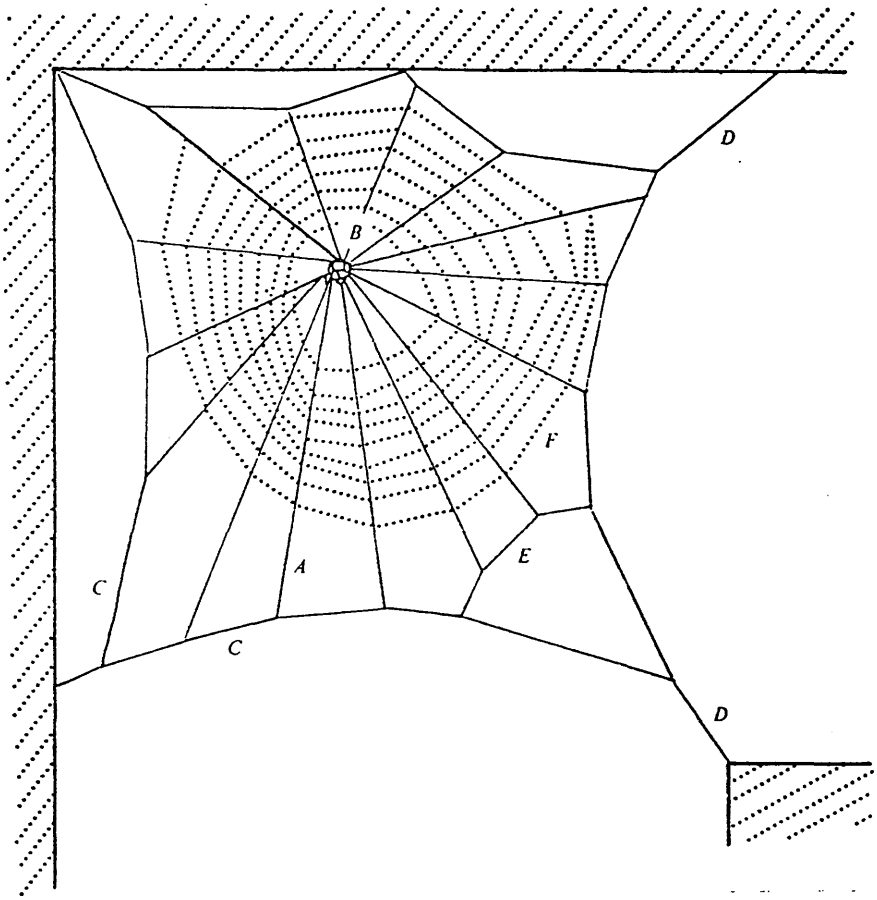

Figure 3.1 Plan of a typical orb web, from Denny (1976). The radii (A) diverge from the hub (B), and attach on the polygonal frame (C). The frame is held in position by the mooring threads (D), which tie the web to the surrounding structure. A cord (E) is spun as part of the frame. The catching spiral (F) is superimposed on this supporting framework. The spiral is viscid in the ecribellate orb spinners, and made from cribellar threads in the cribellates.

glands have spigots on the appropriate spinneret (e.g. Apstein 1889, Warburton 1890). The role of some glands has been deduced by their presence or absence in spiders belonging to groups which have different ranges of silk functions. This can be extended to comparison between the two sexes and between adults and juveniles of one species. For example, only the females spin cocoons, and some adult males of the orb-web spiders do not spin webs (Peakall 1968). Other workers have compared the amino-acid composition of the silks and gland-contents (e.g. Peakall 1969, Andersen 1970), or the reaction of the glands and silks to various stains or digestive enzymes (e.g. Kavanagh and Tillinghast 1979). The final method is to identify, by serial sectioning, which glands are empty after the spider has performed a particular behaviour (Peakall 1964).

There is, however, still a certain amount of disagreement between authors who have attempted to relate silks to the glands that secrete them. Some differences can be accounted for by incorrect nomenclature or description of glands. For example, Peakall's (1964) description of an aggregate gland is claimed by Mullen (1969) to fit that of an aciniform with a section through the coiled tubules of an ampullate. The flagelliform gland, whose function is described as producing the core fibres of the sticky-spiral, was not described until 1952 by Sekiguchi in Japan, and even now there is some debate as to its validity. Peakall (1968) doubts that this gland should be classified separately from the aggregate glands, and in his 1969 paper claims that the sticky-spiral core fibres are derived from the ampullate glands. Mullen (1969) claims that in *Araneus sericatus* there are three different pairs of ampullates, rather than two. He can not separate the functions of the three. However, his third, and smallest ampullate, whose spigot is on the posterior spinneret, could well be the flagelliform gland of other workers. Kaston (1964) proposes that the piriform glands produce the finer fibres of the dragline and frame threads, but Peakall (1968) finds no evidence to support this view.

The origins of various silk-types produced by *Araneus*, deduced from the best supported of these arguments, is given in table 3.3.

Table 3.3. The uses of of the silks produced by the 7 glands of *Araneus*. The middle column gives the spinneret(s) that the ducts from each of the glands leads to. The table represents the scheme which seems to me to be the best supported by the arguments presented in the following papers - De Wilde (1943), Peakall (1964, 1968 & 1969), Lucas (1964), Kaston (1964), Mullen (1969), Andersen (1970), and Kavanagh & Tillinghast (1979).

GLAND	SPINNERET	USE
Major Ampullate	Anterior	Dragline, web frame and radii
Minor Ampullate	Median	Dragline, Web frame and radii
Piriform	Anterior	Attachment disc
Aciniform	Median & Posterior	Swathing bands
Tubuliform	Median & Posterior	Cocoon (Female only)
Flagelliform	Posterior	Core of sticky-spiral
Aggregate	Posterior	Viscid glue of sticky-spiral

The hunting spider *Pardosa* (Lycosidae) produces no catching web, and consequently has only five types of gland (Richter 1970) - ampullate (major and minor), piriform, aciniform and tubuliform. The uses are probably the same as for the araneids, where applicable. But by looking at silk production during the less well studied behaviours of courtship and mating, further uses of the piriform and aciniform silks in both males and females have been found (Richter 1970). For example, aciniform gland silk is used in the outer wall of the cocoon (tubuliform silk makes up the inner wall), and the sperm web of the male. The female constructs her cocoon whilst in a silken retreat made of piriform silk.

According to Kaston (1964), the Theridiidae have a similar range of glands to the Araneidae, but in the former the aggregate glands, which appear to produce the viscid globules of the mooring threads, are larger. Gertsch (1949) describes the glands that produce swathing bands in this family as lobed. Like the aciniform glands that produce swathing silk in the orb-spinners, the ducts of the lobed glands open at spigots on the posterior spinnerets. Hence the lobed and aciniform glands probably are homologous structures. However, the Theridiids produce a lot more swathing silk than the other families, throwing copious amounts over their victim before the spider bites the insect, injecting poison to kill it.

The situation in cribellate spiders is inevitably complicated by the production of cribellate silk. Kovoor & Peters (1988) identify 9 types of silk gland in the uloborid *Polenecia producta*, but fail to provide evidence of the function of each. The glands are as follows: the major and minor ampullates, piriform, aciniform A & B, tubuliform, cribellar, paracribellar and pseudoflagelliform. The first six are similar in position, structure, and apparently also function, to their counterparts in the Araneidae, while the last three are not found in any ecribellate family. The cribellar glands supply silk to the cribellum, to form the fine fibrils of the hackle-band. The paracribellar glands secrete silk *via* the median spinnerets, probably to attach the catching strands to the substrate (Peters 1984).

The pseudoflagelliform glands produce the axial fibres of the hackle-band, *via* the posterior spinnerets, showing a functional similarity to the araneid flagelliform glands. These glands have not been found in the Dictynidae of Fillistatidae, the axial fibres of which probably originate from the ampullate glands.

The hackle-band of cribellate spiders is thus a wool of cribellate fibrils, combed from the cribellum, and placed around one or two axial fibres. Early scanning electron microscopy (SEM), by Lehmensick & Kullman (1957), revealed the diameter of the fine fibrils to be around 0.015μ. Friedrich & Langer (1969), again using SEM, showed each fibril to consist of a central electron-dense filament of 0.003 - 0.006μ diameter, embedded in a less dense matrix, creating an overall diameter of 0.02 - 0.03μ. Similarly, Peters (1984) gives capture thread breadth for Uloborids at 200μ, consisting of an axial fibre of 0.5μ, surrounded by cribellar fibrils 0.025-0.035μ in diameter. These cribellar fibrils are gathered together into woolly patches termed "puffs", regularly spaced in an array around the axial fibres.

Foelix & Jung (1978) describe the cribellate silk of the 'primitive' cribellate spider *Hypochilus* (family Hypochilidae) as consisting of a pair of axial fibres, plus one or two marginal threads which act as a framework for the fine wool.

A spider family that produces a larger range of silks, opens up more possibilities for birds to exploit than a spider family with a more limited range of glands. Furthermore, more combinations of silk-types can be utilised in the constructions of spiders possessing more silk glands, again creating more variation for the birds to exploit. Hence we might expect some families to be have their silk used by birds in their nests more frequently or in more roles than other families. For instance, the Araneidae have around 7 different glands, so 7 silk-types, and the Theridiidae have 6 or 7, while the Lycosidae have only 5 different glands. So, if other factors such as availability were equal, we might expect to find more araneid and theridiid silk in birds nests than lycosid silk. Cribellate spiders use a very

different structure for their capture threads, so again we might expect to find the roles of cribellate web and ecribellate web in bird nests to be different, since they offer rather different properties. The exact nature of these differences is discussed in section 3.4.

However, many silk glands, such as the tubuliform and piriform glands, show a large degree of similarity between families. Their silk also assumes similar roles in the spiders' natural history. Thus, the same silk-type from different families could be expected to have similar properties, particularly in the phylogenetically closer groups. The amino-acid sequence of the silk fibroins, which determines the silks' properties is discussed in the next section. If these properties are indeed similar, birds need show no preference for the silk of one family on this basis alone. How these silks are combined to produce multi-stranded threads and how these threads are combined to produce the various structures, may differ more between families, and this is where a bird's preference could be exercised.

3.2.2. The orb web - an example of different silks in one structure

The structure of an orb web is very similar in both the cribellate family Uloboridae and the ecribellate families Tetragnathidae, Metidae and Araneidae. Typically, mooring threads attach the web to the substrate, while frame threads, usually continuous with the mooring threads, provide the outline. Radial threads run from more or less regularly spaced points on the frame, to the centre or hub. The hub is reinforced by means of the hub spiral, made up of dry silk. The sticky spiral (cribellate spiral in Uloboridae) is laid down toward the periphery. Figure 3.1 gives the structure of such a web (after Denny 1976).

Kavanagh & Tillinghast (1979) describe the structure of the threads as follows. The mooring and frame threads are composed of 8-10 paired silk fibres from the major and minor ampullate glands. The radii consist of two pairs of fibres - one pair from each pair of ampullate glands. The hub spiral is again derived from major ampullate silk, as is the

hub itself. The spiral in Araneoidea, is composed of flagelliform silk with a coating of viscid droplets. In Uloboridae, the spiral is derived form the hackle band silk previously described. Variation in the number of fibres in each thread could account for much of the variation in thread thickness evident from the literature. Therefore, a bird, if it were able, could choose which orb web to take for its nest on the basis of the number of fibres per thread, or upon the type of capture spiral present.

The junctions between threads have been examined microscopically by Jackson (1971) and Eberhard (1976). It appears that there is a cementing substance in most junctions, but those connecting radii and spiral threads in Araneidae are looser, and called sliding connections by Eberhard. The junctions do not break when a strain is placed upon them, rather the spiral thread slides past or through the radius, thus increasing the effective extensibility of the spiral silk, without reducing its strength. This is clearly a property that could be exploited by a bird using silk as a nesting material, as it gives the web as a unit much more elasticity.

The silk in the spiral of Uloboridae is itself far less elastic than the viscid silk of araneids. However, the fine structure of the hackle band, where the 'wool' of cribellate silk can be unravelled, confers upon it potentially great extensibility. So, although the cribellar silk fibres as individuals do not themselves extend much when pulled, the hackle-band can be as useful as any other intrinsically elastic silk to a bird.

A 'stablimentum' is introduced into some webs of some orb-spinning species. This can take various forms (Eisner & Nowicki, 1983), but is characteristically a highly visible system of loosely spun bands or patches of silk laid out across the web. Its role in the web is debated. It was originally thought to reinforce and strengthen the web (hence the name). Other proposed functions include concealing the spider, disguising the spider, advertising the web to prevent larger animals from breaking it, a moulting platform, or attracting insects. Finally, it may be a relict from more primitive webs, where the function

may have been more important (Nentwig & Heimer, 1987). The stabilimentum, being a rather more dense patch of silk than the bulk of the orb web, could confer upon the web properties far more useful to a bird in its nest. For instance, if it can camouflage a spider, it could provide camouflage for the nest. Or if it reinforces the web, it could accordingly improve the structure of the nest.

There is enormous variety in silk usage by spiders. Different families can produce a different range of silks from a different range of glands, and the silks can be combined in different ways to produce different threads and different spider constructions. Each of these will have its own individual properties, and hence have a different attraction to birds as a nesting material. There can be variation in size, strength, extensibility and adhesion of the silken structures. These variations can be exploited when the materials are used in nests. Silk might take on a wide range of roles.

The extent of the variation in these properties depends in part upon the extent of variation in amino-acid composition of the silk fibres, as discussed in the following section.

3.3) AMINO-ACID COMPOSITION OF SILK

Silk, being a fibrous protein (or fibroin), is a long-chain polymer of amino-acids. The properties of the silk are dependent upon the amino-acid sequence. In the course of attempts to relate each silk to its gland, and to discern the structure of silk in order to explain its properties, amino-acid analyses of several fibre-types has been undertaken. Most studies have concentrated upon the Araneidae. The different fibre-types from one individual have very different amino-acid compositions, but the composition of the same fibre-type between species is remarkably consistent.

In general, all silks, including that of the moulting chamber of the silkworm *Bombyx*

mori, are composed mostly of short-chain amino-acids glycine, alanine and serine - 85% of *Bombyx* silk (Lucas & Rudall 1968) and 50-65% of *Araneus diadematus* silk (Peakall 1968). The amino acid compositions of the gland contents given in the following paragraphs are from Andersen (1970), and those of silks are from the authors stated.

The major constituents of dragline and frame silk from *Araneus* species are glycine, alanine, glutamic acid and proline (Fischer & Brander 1960, Lucas 1964, Peakall 1964), which agrees closely with the ampullate gland contents from the same species. Differences in proportions of the amino-acids given in these papers are not reliable enough to look at variation between individuals of one species since the analytical techniques vary. However, Fischer & Brander (1960) conducted the same analysis on three related species - *Araneus diadematus*, *A. undatus* and *A. cucurbitans* (now *Araniella cucurbitans*) - and all three gave very similar results. Furthermore, Lucas *et al.* (1955) conducted an analysis of ampullate silk from a tropical araneid, *Nephilia madagascarensis*, and also found glycine, alanine and glutamic acid as the major amino-acids, but they did not measure proline residues.

Cocoon silk in all three of Fischer & Brander's (1960) *Araneus* species, and in other studies on *A. diadematus*, is dominated by the amino-acids serine, glycine, glutamic acid and alanine. This composition agrees with that of the contents of tubuliform glands, and with that of cocoon silk of the Araneid *Nephila senegalensis* (Lucas *et al.* 1960). Even cocoon silk from the distantly related family, Eusparassidae, shows a similar amino-acid composition (Lucas *et al.* 1960, on *Torania variata*).

Both swathing silk and the contents of aciniform glands of *Araneus* also show high levels of alanine, glycine and serine, but glutamic acid is not so prominent (Peakall 1964, 1968, Andersen 1970). The contents of the flagelliform gland is dominated by glycine, proline and alanine, which confers exceptional extensibility upon its fibre. The aggregate gland contents are primarily glycine, proline and glutamic acid. This shows a

comparatively low number of short-chain amino-acids, which implies the product is less fibrous than the other silks, but rather more amorphous, and would function more like a glue (Andersen 1970). The major amino-acids of the piriform gland are serine, aspartic acid, glutamic acid and alanine. Like the aggregate glands, the proline levels are comparatively high. This, combined with a low proportion of short-chain amino-acids, again confers a more glue-like than thread-like property upon its silk. This accords well with its suspected use in attachment discs.

Total web amino-acid analyses should give the composition of ampullate, flagelliform and aggregate gland silks combined, due to the presence of frame threads, radial threads, and sticky-spiral core fibres and viscid coating. The relative proportions of the three silk types is neither consistent, nor predictable, but the results of analyses by Fischer & Brander (1960) and Peakall (1964) on *A. diadematus*, showing highest values for alanine, glycine and proline, do support this proposed amino-acid distribution.

The viscid droplets of the sticky-spiral do not contain only amino-acids. Analysis has shown them to contain high levels of phosphate, hydrogen-phosphate (Schildknecht *et al.* 1972) and gamma-aminobutyramide (Fischer & Brander 1960). These are thought to make the protein hygroscopic, preventing it from drying out and losing its stickiness (Andersen 1970).

Amino-acid analysis has helped to confirm which gland contributes to which silk, as given in table 3.3, and given some indication as to what properties to expect each silk to exhibit. The remarkable similarity across groups of spiders should mean that one type of silk from any species will show very similar physical properties, and therefore the birds exploiting these silks as nesting materials need show no preference for one species or group of species based upon the physical properties of the threads. Any preferences may be based on spider ecology - accessibility of silk, abundance of silk, density of threads - or upon the physical properties of the silken structures themselves. Preference should be

shown, however, for silk-type. The amino-acid compositions of the different silks, and hence their physical properties, do show considerable differences.

3.4) PHYSICAL PROPERTIES OF SILKS

The important physical properties of silk that make it such an exceptional biological material are its extensibility, tensile strength and, in some cases, adhesiveness. These are the properties that make silk so useful not only to the spider, but also to birds as a nesting material. Much research has attempted to assess these properties, particularly the first two.

3.4.1 Strength and extensibility of silk

In order to understand how the silk properties can determine the birds' choices as to which silks to use as nesting material, the properties must be quantified. Therefore some definitions are required. The following is based on Wainwright *et al.* (1976). When a force is applied to a body, deforming it, a stress (σ) is exerted, defined as force/unit area of cross-section, and a strain (ε) is induced in the body, defined as the ratio of change in dimension to original dimension, often expressed as a percentage. In the case of work on silks, the stress is applied in the direction of the axis, and the strain is due to a change in length. When calculating stress, the cross-sectional area used must be that during the elongation, which decreases in proportion to the increase in length ($A \propto 1/L$), assuming constant volume.

A curve can be plotted of stress against strain (or force against extension). The slope of such a curve is called Young's modulus (E), defined as σ/ε. However, for silk, force-extension curves are rarely linear over their entire length, so this modulus is dependent

upon the force exerted (figure 3.2). Often two values of E are given - one, E_{init}, for low force, and one for the force applied at breaking, E_{final}. The tensile strength of the silk is this breaking stress. Tenacity is related to tensile strength, but is the breaking force per unit original cross-sectional area. Thus tenacity is the tensile strength divided by the ratio of length at breaking to original length (or $1 + \varepsilon_{max}$, where ε_{max} is the breaking strain - or maximum extension before breakage).

Unfortunately, these values are dependent upon many factors, which are not consistent between workers - e.g. humidity, temperature, and rate of extension (Denny 1976). Some values that have been obtained for extensibilities, tensile strengths and Young's moduli are given in table 3.4. Early work, such as De Wilde (1943), does not specify for which part of the force-extension curve the Young's moduli were calculated.

All the work so far carried out on these properties has been on the Araneidae. Comparisons with other families are not available. However, there is so much variation in values obtained by different workers for similar silks, that such comparisons would probably be meaningless. All the silks studied show remarkably high tensile strength, combined with high extensibility, which make the resistance of the silk to rupture far greater than other natural or man-made fibres (Work 1976).

Three different silk types have been tested - frame/dragline (from ampullate glands), viscid thread (from flagelliform and aggregate glands), and cocoon (from tubuliform glands) - and differences in their physical properties can be distinguished. Dragline and frame silk are the least extensible (around 25-40%), cocoon silk rather more extensible (45-100%), and the catching thread very much more - up to 1600% according to De Wilde (1943) for *Meta* and up to 300% for *Araneus*. Cocoon silk has a much lower tensile strength than frame silk (up to 0.5 GNm^{-2} compared with 0.8 - 1.6 GNm^{-2}), but the situation for viscid silk is less clear. According to Denny (1976), its strength is similar to that of frame silk, at 1.3 GNm^{-2}, but Gosline *et al.* (1986) find it is much lower, around

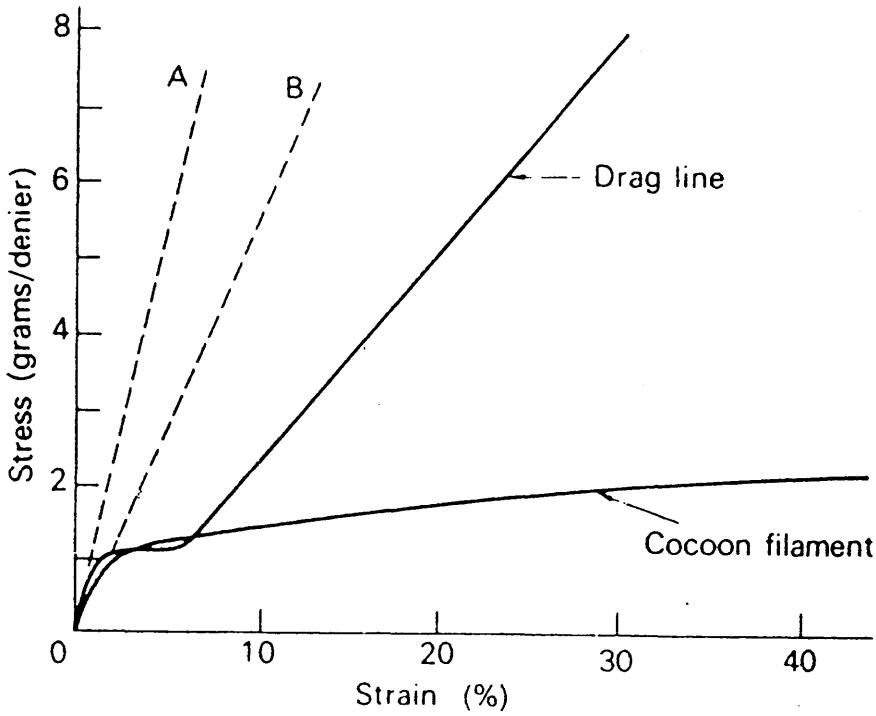

Figure 3.2 Stress-strain curves for two types of silk - dragline and cocoon fibre, from Wainwright *et al.* (1976). Dashed lines OA and OB are the initial slopes (E_{init}) of the dragline and cocoon curves respectively.

Table 3.4 Physical properties of silk. For various species of orb web builders, the properties of some of the silks are given. The type of silk tested is shown in the second column, the conditions under which the tests were made in the next three (relative humidity, temperature and rate of extension, where the information is available), followed by the extensibility, expressed as the percentage of the original length, and the tensile strength measured. The next two columns give values for Young's modulus, E, firstly at the start of the extension, and secondly just before the silk breaks. The name of the worker who carried out the experiments is given in the last column. The silk samples are divided by author.

SPECIES	Silk-Type	rH (%)	Temperature (°C)	Rate of extension 1/min	Diameter (u)	Extensibility (%)	Tensile strength (GNm^{-2})	E_{init} (GNm^{-2})	E_{final} (GNm^{-2})	Author
Araneus diadematus	Dragline (coarse)	room	room	1.0	2.7	32.0	1.6	-	-	
	Dragline (fine)	room	room	1.0	1.2	37.5	1.7	-	-	
	Frame	room	room	1.0	3.1	33.5	1.4	-	-	
Araneus sericatus	Dragline	room	room	1.0	2.7	23.5	1.2	-	-	Work (1977)
	Frame	room	room	1.0	1.4	23.0	1.3	-	-	
Araneus gemma	Frame	room	room	1.0	3.6	33.0	1.4	-	-	
Argiope aurantia	Frame	46-54	20-22	1.0	4.8	35	1.32	5.2	3.2	
	Frame	46-54	20-22	1.0	4.2	32	1.45	5.3	3.7	Work (1976)
Araneus diadematus	Frame	46-54	20-22	1.0	3.0	40	1.60	4.9	3.3	

SPECIES	Silk-Type	rH (%)	Temperature (°C)	Rate of extension 1/min	Diameter (u)	Extensibility (%)	Tensile strength (GNm^{-2})	E_{init} (GNm^{-2})	E_{final} (GNm^{-2})	Author
Argiope argentata	Frame	46-54	20-22	1.0	6.2	42	1.41	5.2	2.8	Work (1976)
Euriophora fuligenia	Frame	46-54	20-22	1.0	5.6	26	1.26	8.6	3.6	
Araneus diadematus	Dragline	?	?	?	?	30	1.42	10.0	4.7	Gosline *et al.* (1986)
	Viscid	?	?	?	?	c 200	0.60	0.003	0.5	
Araneus sp	Dragline	?	?	?	1-3	20-30	c 1.0	<20	-	Denny (1980)
	Cocoon	?	?	?	?	50-100	c 0.5	-- 1.0 --		
Araneus sericatus	Frame	48-52	24	0.03	1.9	25	0.81	9.81	3.52	Denny (1976)
	Frame	48-52	24	1.41	1.9	25	1.42	20.50	4.07	
	Viscid	48-52	24	0.07	1.5	300	1.11	-	0.56	
	Viscid	48-52	24	0.32	1.5	300	1.27	-	0.56	
Araneus diadematus	Dragline	?	?	?	?	31	1.14	-	-	Lucas (1964)
	Cocoon	?	?	?	?	46	0.36	-	-	

0.5 GNm^{-2}. Denny (1976) found that the faster the silk is stretched, the higher the stress that can be sustained. This rate of extension has not often been recorded by other workers, and could explain the large discrepancies. However, the extension rate has more effect upon frame silk than upon viscid silk, even though the latter shows the greater range of values for tensile strength. As for Young's modulus, at low strains, viscid silk is 4 orders of magnitude lower, and at breakage, 2 orders of magnitude lower than frame and dragline silk.

As a nesting material, the suitability of these three basic types of silk - frame/dragline, cocoon and viscid thread, will differ. If strength is the most important property, frame or dragline silk should be chosen in preference to the others. If extensibility is the major concern of the bird, then viscid silk would be most suitable. But if a balanced combination of these two properties is required, cocoon silk provides a compromise.

The overall picture of spider silk properties led Denny (1980) to state 'the silks are unique among natural fibres in combining very high tensile strength with relatively large extensibility. As a consequence, it takes more energy to break a given volume of silk than it takes to break the same volume of any other biological material.' Cases of spider silk ensnaring animals larger than insects are not uncommon. Gertsch (1949) cites examples of small birds being inextricably entangled in webs of the larger *Nephila* species, and even an example of a small *Theridion* lifting a one-and-a-half inch long mouse off the floor by spinning silk around its tail and pulling it up in a manner similar to the block-and-tackle method. This is just one example that serves to illustrate that silk, even from a small spider, can be strong enough to lift a body far larger than the spider itself. The silks' properties may in fact be under-used as a nesting material, binding the structure together. If used extensively in a nest, silk should provide the nest with greater resilience than the forces that the nest may be subjected to demand.

The qualitative differences in properties between the three types of silk are in

accordance with the probable amino-acid compositions of the gland contents and silks given in section 3.3. For example, the contents of aggregate glands and the core of the viscid threads of Araneidae have a high proportion of long-chain amino-acids, and as predicted, the fibre is exceptionally extensible. On the other hand, cocoon silk is more dominated by the short-chain amino-acids, and its extensibility is closer to that of silk from the major ampullate glands. If the silk of the minor ampullate glands follows this pattern, then it should have extremely low extensibility, together with low tensile strength (Andersen 1970). Gosline *et al.* (1986) argue that minor ampullate fibres reinforce those of major ampullate glands, but the properties predicted do not support this view. Furthermore, Kavanagh & Tillinghast (1979) state that the pair of minor ampullate threads can easily be pulled away from the pair of major ampullate threads in the radial thread of *Araneus*.

3.4.1.1 Determinants of thread diameter.

Thread diameter may directly affect a bird's choice for its nest, since the actual strength of the thread is directly related to the diameter - strengths are normally expressed as sustainable force per unit cross-sectional area. Although, in common with other man-made and natural fibres, finer silks have a stronger specific strength, the total sustainable force will be greater for a coarser fibre.

As can be seen from table 3.4, the values for diameter of a particular type of strand show great variation. Values given in the literature for a single strand of frame and radius silk of *Araneus diadematus* adult females range from 1 μ to 9 μ (e.g. Jackson 1971). Wilson (1962, 1969) has shown that spiders of the Uloboridae, Tetragnathidae, Araneidae and Theridiidae have a valve in the duct of the ampullate glands, and by altering the diameter of the valve by valve-tensor and duct-levator muscles, together with adjusting the intra-abdominal pressure, exercise fine control of the rate of dragline production, and diameter of fibre produced. Therefore, the diameter of the fibres recorded in table 3.4, will be dependent upon the internal state of the spider when the silk was being produced, the rate

of its production, and the purpose of the silk, since different parts of the web are built of threads of different thicknesses (Christiansen *et al.* 1962). Also, Jackson (1971) found that the thread thickness varies greatly within one thread, particularly in the region of a junction with another thread. Further confounding any comparisons is the fact that the measured thread diameters will depend upon the temperature and humidity in which the measurements were taken (Work 1977), and upon the tension under which the strands are held (Christiansen *et al.* 1962).

A bird may be unable to assess directly the diameter of a thread, but may use an indicator, such as the size or species of spider that spins the web, or the size of the web.

Attempts have been made to correlate silk diameter with spider size or weight. The theory is that a heavier spider needs a stronger, hence thicker, thread to support it. If material is limiting, the length of the threads produced will necessarily be shorter. Christiansen *et al.* (1962), by adding weights to spiders, found a weight increase of 30% doubles the weight of protein per meter of thread, whilst decreasing total web thread length to 67%. This in turn would change such web parameters as number of radii (fewer), number of spiral turns (fewer), and mesh size (larger). These differences, or their consequence upon overall web geometry, may be the ones used by birds to assess thread diameter, and hence strength. It should be noted that Witt *et al.* (1972) provide evidence supporting a genetic component, in addition to spider weight, to the variation in web geometry, and by implication, possibly also to thread diameter.

A bird could also use would be web size itself to indicate thread diameter. A larger web is generally spun by a larger spider, and so the constituent threads are generally coarser.

Another variable that may influence web geometry is the internal state of the spider. Reed *et al.* (1970) found that *Araneus diadematus*, when kept in a confined space where

web construction is impossible, builds a web of smaller size, and sometimes larger mesh-size, using a shorter length of thread. The thickness of the threads of the aberrant webs were not measured. Thus, it could be the case that stress in spiders, as a result of such factors as hunger or temperature, may in some way produce effects parallelling those of many drugs (see Witt and Reed, 1965, and Christiansen *et al.*, 1962, for examples). Internal factors do influence web geometry, and may affect thread diameters as well. This would make the choice of silk by birds based on spider size to an extent unreliable.

The other possible indicator of thread diameter could be spider species. Craig (1987a) showed a strong correlation between the average viscid thread diameter and the average body weight of five species. However, the cross-sectional area of frame silk showed no significant relationship with body weight. Indeed, Work (1977) showed that individual ampullate fibres from a single web can have a wide range of diameters, with no correlation of fibre diameter with body weight. Craig (1987b) goes further to say that there is no relationship between spider weight and thread tensile strength, and no predictable relationship between spider weight and thread extensibility. If this is the case, then birds' choice of silk based on spider species to predict thread diameter, would be invalid.

Silk diameter does vary with size, weight or age of spider, though other factors obviously play a part. This has implications for availability of suitable silk during the birds' breeding season. Those spider species that mature in early spring (*i.e.* overwinter as a sub-adult) may be used more in nests than those that are juveniles or hatchlings during this season.

Work has also been carried out on the cribellate family Uloboridae. Cribellate silk puffs, aligned along the core of paired axial threads, were measured by Opell (1989), who found that puff width and length both correlated with the width of the cribellum. However the width of the cribellum is not predictable from body size or body weight. This is not necessary for the spider since cribellate silk is not used to support the spider. How the

properties of cribellate threads with puffs of different sizes differ is not documented. However, a bird's choice for its nest may be based upon puff size, since this is a function of both the cribellar fibre diameter and the amount of cribellar silk present.

3.4.2) Adhesiveness of spider silk

Adhesiveness of spider silk is the third property making it so unique. Attempts have been made to compare this property between families. Strohmenger and Nentwig (1987) compared the webs of a primitive ecribellate Orthognath, *Ischnothele guyanensis* (Dipluridae), a dry-webbed ecribellate, *Tegenaria atrica* (Agelenidae), a viscid-webbed orb-weaver, *Zygiella x-notata* (Araneidae) and a cribellate *Filistata insidiatrix* (Filistatidae). Only the web of *Zygiella* adhered at all to smooth paper, but all adhered to the more irregular surface of filter paper. *Zygiella* web adhesion was severely reduced by being dried or dusted, but neither treatment affected the other three webs, demonstrating the effect of viscid droplets. The lower density of threads in an orb web compared with the other three meant that it was two or three times less adhesive to the filter paper. The web of *Tegenaria* proved to be the most adhesive to filter paper, but the cribellate web of *Filistata* was capable of trapping the widest range of insects.

These findings are in disagreement with those of Eberhard (1980), who showed that, although adhesiveness is not reduced by drying, cribellate silk of *Uloborus* loses its adhesiveness in nature due either to rain or to dust accumulation. Kullman (1975) has clearly shown that adhesiveness of cribellate silk is not due solely to the fine fibres of the hackle band entangling substrate irregularities. However, there is no sticky substance on the cribellate threads (Foelix and Jung 1978). Many accounts of cribellate silk (*e.g.* Bristowe 1958) say that it has a bluish hue when freshly spun, but this is less distinctive in older threads. If, as is currently believed (*e.g.* Jones 1983), the colouration is due to the fine structure of the cribellate silk, rather than colouration of the fibrils, then this fine structure is presumably deteriorating with time. Peters (1987) expects considerable

species-specific differences in persistence of stickiness. Loss of adhesiveness, according to Peters, is due to the irreversible collapse of the puffs.

According to Foelix and Jung (1978), fresh cribellate silk will adhere to a clean, smooth glass slide, but older silk will not, again indicating the existence of adhesiveness that is not due entirely to entanglement. Whatever the cause of its adhesiveness, cribellate silk should be extremely useful as a nesting material, having an element of adhesiveness that is very persistent, as well as possessing a high degree of extensibility.

The situation regarding persistence of adhesiveness in the viscid threads of orb webs is clearer. Schildknecht *et al.* (1972) have shown the presence of hygroscopic chemicals in the glue, which decrease the likelihood of the glue drying out. The acidity of the chemicals (pH = 4), probably reduces attacks by bacteria and fungi (Foelix 1982). However, in spite of this, and of the strength of orb webs, Breed *et al.* (1964) demonstrate that the reason for frequent web replacement in the Araneidae is web deterioration. As Strohmenger and Nentwig (1987) show, the adhesiveness does decline when the silk is dusted. Furthermore, Eisner *et al.* (1964) and Nentwig (1982) have shown that many insects escape capture in the viscid threads by shedding scales (in the case of Lepidoptera) or hairs, leaving these attached to the threads, which therefore lose their catching properties. Rain will remove the water-soluble viscid coating (Peters, 1987), but generally, rain destroys the webs' structure too (Robinson & Robinson 1973). Overall, therefore, the value of orb web silk as a nesting material is very much reduced by this rapid loss of adhesiveness, even if at collection the viscid threads are in good condition.

The short operational time of orb webs necessitates frequent web-replacement. Peakall (1971) has shown that replacing a web every day or so is not wasteful, since the old web is digested. Rapid and frequent replacement means that the supply of orb webs available to birds, providing the spider itself is not eaten, is renewable on a daily basis. One orb-spinning spider, from America, *Cyrtophora moluccensis* builds a far more persistent web. It

is denser, stronger and non-adhesive (Lubin 1973). This web is a less efficient insect trap, but its unusual properties may make it a valuable nesting material.

3.4.3) Summary of the properties of silk

Silk is a very strong and extensible material, the different types showing these properties to differing extents. Thread diameter, upon which the strength is dependent, varies with spider size, though not predictably. There are various means by which a bird could predict thread diameter. Adhesiveness, the third important property of silk, declines with the age of the silk, but cribellar fibres seem to be more persistently adhesive, and a more efficient binding material, since it can trap a wide range of insects.

The families show variation in their use of silk in webs, retreats and cocoons, and this will be variation available to birds. The next section deals with the silken structures built by spiders.

3.5) SILKEN STRUCTURES

The structure of cocoons, retreats and webs could show differences that may affect a chaffinch's choice for use in her nest. Very little work has been carried out on the structure of cocoons and retreats, but the structure of webs of the different families have frequently been described, and the orb webs of Araneidae and Uloboridae have been studied in detail, as discussed earlier.

The structure of cocoons shows much variation amongst the spiders, from eggs tied together by a few single strands of silk, to intricate sacs with two or three distinct layers of silk. In general, the degree of protection offered by the cocoon's structure is related to the extent to which it is vulnerable to destruction (Gertsch 1949). So if the cocoon is hidden in

the mother's burrow, or by barriers of dense web, it is not usually strongly constructed. Also, if the mother guards the cocoon by remaining with it, or carrying it with her, until the young emerge, there is less need for it to be strong (Gertsch 1949). These weaker cocoons are mostly built by the non-web building species.

Cocoons of web building families receive less protection by the behaviour of the mother. Normally the female dies fairly soon after oviposition (Turnbull 1973). In these cases, cocoons must be constructed so that they are impenetrable to predators and parasites, and provide protection against the elements. Hence a common form in the Araneidae, consists of a soft lining layer in which the eggs are suspended, surrounded by a loosely-packed insulating layer, and the whole enclosed in a tough, papery outer layer (Turnbull 1973). Two different types of thread, with different diameters, are involved - one forming the loose matrix in which the eggs are suspended, the other the covering envelope. The source of the enveloping threads is not documented, but the tubuliform glands supply the matrix threads.

There is usually no one type of cocoon typical of a family, but taxanomically, according to Holm (1940) the Haplogynae (Scyotidae, Oonopidae, Dysderidae, Pholcidae) tend to have the simplest form of cocoon, the Dionycha (two-clawed families, such as Clubionidae, Thomisidae, Salticidae) have a tough thin-walled cocoon, and the Trionycha (three-clawed families, such as Lycosidae, Theridiidae, Araneidae, Linyphiidae) have an egg-sac surrounded by a thick layer consisting of a loose meshwork of threads. However, the validity of even this basic difference is at best dubious, since the monophyletic origin of the Dionycha or Trionycha is not confirmed. The Dionycha tend to be non-web building families, and the Trionycha are typically web builders (Preston-Mafham and Preston-Mafham, 1984), but no reasons are given for supposing any evolutionary relationship. Furthermore, secondary reduction of cocoon complexity can occur to suit the spider's life-style (Foelix 1982), so confusing the issue even more.

Although cocoon design is not helpful for recognising spider families, cocoon colour is often characteristic of family (Kovoor 1977). For example, those of the Thomisidae and Gnaphosidae are generally white, while those of the Tetragnathidae are more or less dark green. However, in the Lycosidae, colour varies between genera, or even species. White, yellow, brown, green or blue are the usual colours, but this may well depend upon the immediate environment where the cocoon is spun. In the Araneidae, groups of related genera have their own particular colour and texture of cocoon. There is also evidence that the colour of cocoons changes with time. Over several hours after the silk has been spun, the colour may develop from white or yellow, to browns or blues *etc.* This change is brought about either by absorption of moisture from the atmosphere, or by oxidation (Bristowe 1958).

Similarly, the colour of web silk can be characteristic of species or genera. Examples cited by Kovoor (1977) include *Nephila* (family Araneidae) webs contain silvery-white frame and radial threads, but the spiral is bright yellow or gold. The web of the Brazilian Araneid *Cyrtophora sellata* is golden yellow.

In their family-by-family accounts of spider biology, Gertsch (1949) and Bristowe (1958) describe cocoons for various members of the families, but do not attempt any generalisations. Furthermore, differences between species are unlikely to affect a bird in selecting a cocoon for its nest since the structure has to be disturbed and partially destroyed during the removal of the cocoon from the substrate to which it is attached. One might expect, however, that those families that spin cocoons consisting of a large meshwork of threads would be favoured for structural purposes over the thin-walled cocoons typical of the Dionycha, since there is a greater amount of silk and more variability in the type of silk in one cocoon in the former group. Where the cocoon is used for camouflaging the nest, birds may favour those colours that make the nests least conspicuous against the background of surrounding vegetation. For example, North (1904), in his review of Australasian birds' nests, frequently mentions green spider

cocoons as a nesting material decorating the outside of the nest (*e.g.* monarch flycatcher).

The cocoons of few families have been examined methodically. Opell (1984) examined cocoons of the Uloboridae. The eighteen genera show diversity in the shape and placement of eggsacs. He looked at the structure of cocoons from seven of the genera. Mostly they were composed of a lining of fine silk (diameter of 0.9 - 1.2μ), with an outer layer of coarse silk (diameter of 1.4 - 1.9μ). However, some species had a coarse silk lining or a fine silk coating. In addition, *Hyptiotes* had a layer of much coarser silk (5.6μ) extended into pointed tufts above the cocoon surface. Colours found included white, tan, light pink, and shades of grey. There is, therefore, within one spider family, enough variation in cocoon structure and colouration to enable a bird to distinguish between species and show preference for one or more.

3.5.1) The webs, retreats and cocoons of 7 important families.

A generalised picture of the silken structures spun by the families likely to be found commonly at Garscube Estate, and how the silk could be used by birds as a nesting material, is given below. The colour, shape, positioning and size of structures, together with the amount of silk used in them, is considered for cocoons, retreats and webs of seven families. The information is compiled from family overviews in Gertsch (1949), Bristowe (1958), Foelix (1982) and Preston-Mafham and Preston-Mafham (1985).

LYCOSIDAE

The cocoon is more-or-less spherical in shape, with strong silken walls and tightly wrapped in bluish green of yellow/brown silk threads (Gertsch 1949, Bristowe 1958). It is carried by the female attached to her spinnerets until the young emerge.

The retreat is a silk-lined tunnel in the soil, often very much reduced. The colour of the silk is not recorded in the available literature.

There is no web built by members of this family.

This family provides a poor source of silk for bird nest-building: No web is built, and the retreat silk is inaccessible; the cocoon can only be obtained by catching the adult female, who will to her best to avoid losing her progeny.

AGELENIDAE

The cocoon consists a lens-shaped egg-sac covered with silk in which are placed bits of bark *etc* as camouflage and hidden in a secluded place such as under tree bark. The amount of silk in the egg-sac is not recorded, and the camouflage hides any colour.

The retreat is a funnel-shaped tubular structure, leading into crevices or corners in walls, fences or trees. It can be very expansive and is an extension of the web.

The web itself is a flat irregular sheet of extensive densely-woven non-viscid silk. It is situated across corners and crevices and is more-or-less white in colour.

As a source of silk for bird nests, both the large, dense web and retreat could be useful. Furthermore, where the cocoon is less well hidden, such as up against a wall (Bristowe 1958), and is more accessible to the bird, it could also be used.

THERIDIIDAE

The cocoons are usually more or less spherical, with the envelope spun while the sac is being rotated, producing a very even surface to the thick wall. The size varies between species from far smaller than the female to larger. They may be placed in the web, gummed in a corner or crevice near the web, in the female's retreat, or in a curled leaf (Bristowe 1958). Cocoons are made of either white or coloured silk. Some species make no attempt to conceal the cocoon, and suspend it in their web. *Theridion bimaculatum*

carries her cocoon attached to her spinnerets. The cocoons of *T. pallens* are knobbly and larger than the female.

The retreat, in those species that construct one, is a small conical tent, camouflaged with detritus, at the edge of the web. The amount of silk contained in the structure is not documented.

The extensive 2- or 3- dimensional irregular web that is typical of this family, is constructed from threads placed very sparsely. The mooring threads are partially covered by viscid droplets in several species. The web is strung amongst twigs in bushes or close to flat surfaces, such as walls, where it becomes quite flattened.

Both cocoon and retreat could provide a useful source of silk, but the sparse lines of the web contain very little silk, making them less useful than the webs of the sheet-builders.

ARANEIDAE

The cocoon is irregularly shaped and slightly flattened, and consists of a cemented mass of eggs surrounded by a thick cover of relatively loosely-woven coarse yellow silk. Over this structure, and anchored to the substrate, is a further layer of coarse threads, usually white (Bristowe 1958). The cocoon is placed at the edge of the orb web in crevices or pressed into corners.

The retreat is elongated and flattened, and is a tough, thin-walled, papery structure, sometimes with a loose meshwork of threads underneath. Like the cocoons, retreats are located at the edge of the orb web, or in crevices (pers. obs.), and the cocoon sometimes is located within the retreat.

The orb web is sparingly constructed of various types of silk, as described earlier,

including viscid threads in the catching spiral. It is designed to present the most efficient catching area using the least amount of silk.

One feature of orb webs of the Araneidae, in addition to those discussed previously, is the nature of the junctions between threads. In particular, those between radial and spiral threads allow the threads to slide relative to each other. This increases the affective extension of the threads when they are pulled, and prevents the spiral from become detached from the radii, though the breaking strain is unaffected. Overall, this property acts to strengthen the web and increase its overall extensibility when stretched by a bird as it is incorporated in a nest.

The orb web is usually strung across corners and amongst sparse foliage.

Where the cocoon is more accessible, it could provide a very good source of silk for birds' nests, but the retreat is probably too thin-walled to be of much use. The orb web probably contains too little silk to be worth collecting by birds, in spite of the large proportion of sticky threads. In any case, silk rapidly loses its adhesive properties. It is possible that in the larger tropical *Nephila* species the webs contain enough silk to enable birds to exploit the great extensibility and strength, and the range of silk properties offered in an orb web.

METIDAE

This family is very similar to the Araneidae in all aspects except for the cocoon. The cocoon is globular, thick-walled, and composed of tightly spun silk, white in colour. It is suspended on silken threads from twigs *etc.* These are on the whole more accessible than those of the previous family, but are well hidden amongst vegetation. The same points as for Araneidae regarding usage by birds apply.

LINYPHIIDAE

In spite of being the largest and most abundant family in Britain, the cocoons and retreats of this group have been studied very little. Indeed, in their general accounts of spider biology, Gertsch (1949), Bristowe (1958), and Foelix (1982) do not mention these structures.

It seems that no retreat is constructed, but the spider lies underneath the web at the edge, waiting for prey.

The web is a sheet of dense silk, possibly slightly viscid, usually found in bushes and tree twigs near to the ground. It can be very extensive when built by the larger species.

The webs, especially larger ones, might be ideal as a nesting material for birds.

AMAUROBIIDAE

The cocoon is a small flattened egg-sac, concealed in the female's retreat under tree bark, or within wall crevices. No information is given in the available literature on the amount of silk involved, or its colour.

Retreats are only spun by females, and only while egg-laying. They are situated under tree bark or in wall crevices, and are composed of white silk Precisely what constitutes a retreat in this family, and the extent to which the retreat is separate from the web is not documented.

The web is a large, dense, irregular sheet, like a funnel leading to the spider's shelter. It incorporates cribellar catching threads, and forms a layer over tree bark or walls. The cribellar threads give the web a characteristic bluish appearance when fresh. The web is added to nightly, rather than removed periodically and rebuilt, so the overall extent of the web is independent of spider size.

The retreat-cum-cocoon of this family is probably too well-concealed to be of much use as a nesting material. However, the cribellate webs should provide ideal material for birds nests, containing a lot of silk in a small area, and the capture threads retain much of their adhesive properties for a long time.

Summary

In summary, the best sources of cocoon-silk would appear to be those agelenid cocoons that are less well concealed, and cocoons built by members of the Theridiidae, Araneidae and Metidae. The range of cocoon types and positions exhibited by these families make representatives of all seem possible as sources of nesting material.

Retreats used might be expected to belong to the agelenids or the larger theridiids, since the silk is in thick layers and relatively accessible.

The best web-silk sources would apparently be the sheet webs of Agelenidae and larger Linyphiidae, together with the cribellate sheets of Amaurobiidae. In these families, each web can provide a reasonable quantity of silk whose properties are designed to trap and hold other materials. Furthermore, they are placed in accessible positions. We saw in section 3.4.2 that webs of cribellate spiders trap a larger range of insects than the other types of web, while webs of the Agelenidae attach more firmly to filter paper. These are two indications that these webs, which do not rely on glue-like substances, may be the best available to birds.

The large range of structure-types that make this overview so generalised, also make the process of identifying silk samples used in nests very difficult. Cocoon structure may give clues to the family or even genera of origin, but after the birds have manipulated them in the nest, much of this structure may be lost. Identification to family of web material may be possible, particularly in distinguishing the Amaurobiidae from the others

due to the presence of fine cribellar silk. Sheet webbing could be distinguished from orb or irregular webbing purely by the bulk of material involved. Beyond this level of classification, distinctions between genera probably will be too fine to be reliable.

CHAPTER 4

INTRODUCTION TO INVESTIGATIONS OF CHAFFINCH NESTS AND SILK

We have seen that silk is a very useful material and available to birds in varied forms. We have also seen how chaffinch nests are designed, and the potential for silk use. We have seen how important a good nest structure, built in a short time, is to the chaffinch, and some of the constraints the birds are under. This study is investigating how chaffinches use silk, what types of silk it uses, and how the use of silk may affect other aspects of chaffinch breeding biology

By gathering nests from throughout the United Kingdom, and conducting a year-round study of the silk availability in a site on the edge of Glasgow, the following questions were examined. these questions.

1. How much silk is used in nests, and how much variation in silk content exists between nests? Does the use of other materials require, or obviate the need for, silk? This leads onto questions of precisely how the silk is used in nests.

2. Which of the following possible uses of silk are exploited by chaffinches: binding the structure of the nest; binding the materials of the superficial layer to the foundation; attaching the nest to the bush or tree; or acting as camouflage? By looking at the materials each silk unit is attached to, we can decide which of these are valid.

3. Are there differences in the preference of chaffinches for three broad categories of silk unit - web, retreat and cocoon - for use in their nests, and are these silks employed in different roles in the nest? By examining silk samples taken from the nests, and comparing them with silk samples taken in the wild from identified spider species, it may be possible to determine which spider species are the most important for nesting chaffinches.

4. Is it possible that the timing of chaffinch nesting and the location of chaffinch territories could be influenced by the availability and distribution of the more important silk types in the environment? Further, could such factors have implications for the way in which the birds go about collecting the silk they need.

CHAPTER 5

MATERIALS AND METHODS

5.1) STUDY SITE

In order to study fluctuations in silk availability through the year, and to find nests where the types of silk available to the chaffinches was known, Garscube Estate in Glasgow was chosen as the study area. It is parkland covering an area of 1200 hectares, containing a variety of habitats: dense woodland, with both deciduous and evergreen trees & bushes,
rhododendron bushes, meadowland for grazing animals, mowed grassland, hedgerows, and old and modern buildings, including farm buildings and disused sheds. The river Kelvin runs through the Estate and forms one side of the part of the Estate involved in this study. The other boundaries are roads on two sides, and houses on the fourth. Figure 5.1 is map of the area.

5.2) TIMING OF CHAFFINCH BREEDING AT GARSCUBE ESTATE

Between 3rd April and 19th July 1990, observations were made of the behaviour of chaffinches at Garscube Estate (dates given in table 5.1). This were compared with observations of chaffinch behaviour during the breeding season as described by Marler (1956) to decide at which stage of the breeding cycle the chaffinch population was at the time of observation. Behaviours looked for were: in males, territorial singing and fighting,

Table 5.1 The dates on which the breeding behaviour of chaffinches at Garscube Estate was studied. These are also the dates of the search for in-use chaffinch nests was carried out.

April 1990	May 1990	June 1990
3, 13, 16, 24, 25, 30	3, 7, 8, 11, 14, 15, 18, 22, 23, 25, 29	1, 5, 15

and attempting copulations; in females, searching for possible nest sites, collection of nesting materials and nest construction, soliciting copulations, and brooding; and in both sexes, copulation, collection of food, and feeding of fledglings. Their occurrence, and the pair involved, were noted against the date of observation.

5.3) INVESTIGATION OF CHAFFINCH NESTS

5.3.1) Sources used to obtain the nests

Chaffinch nests for this study were obtained from four sources:

i) Search by myself, friends and members of staff and students at Department of Zoology, University of Glasgow in and around Glasgow and in other parts of Great Britain. Eight people other than myself were involved in this, but the amount of time spent by each is unknown. 9 nests were found. My own search at Garscube Estate outside the breeding period, occupied around 15 hours between 4th October and 13th December 1989, but revealed no nest.

ii) Nests borrowed from the Royal Scottish Museum in Edinburgh, and the Kelvingrove Art Gallery and Museum, Glasgow. Three nests were supplied by the Royal Scottish Museum, originating from the Lothian area of Scotland. Kelvingrove Museum, supplied 8 nests originating from various areas in the west of Scotland. Many of the museum nests lacked information on the habitat type in which the nests were found, and some also lacked the year of discovery. The oldest nests were found in 1877.

iii) Appeal in BTO Newsletter in January 1990 for BTO members to send any nests they find from the 1989 or 1990 breeding seasons. This produced 15 chaffinch

nests. These came from areas of the United Kingdom as far apart as the south-west of England, north-west Wales, Northern Ireland and the north-east of England. Information supplied with these gave the date of discovery, the location, the habitat type, and the type of vegetation in which the nest was built. The condition of the nests was variable. Some had become squashed and the structure of them partially destroyed in transit, and others had been damaged before collection. Many had not been completed, lacking a lining, and some even lacked much of a superficial layer. In the latter cases, the superficial layer simply may have not been constructed by the chaffinch, or it may have been destroyed at some point after it had been constructed. Alternatively, the nest may have been abandoned before the stage of construction of the lining or superficial layer had been reached.

iv) Mapping and searching territories at Garscube Estate for 1990 season nests. Territories were located using methods based on those of the BTO national bird census. The method consisted of walking the area, listening for male chaffinch songs and locating the singer, an idea of the location of boundaries between neighbouring territories is built up. Male singing is at its peak early during the breeding season. During the nest-building period, when the females make trips to and from the nest most frequently, the female in each territory can be quietly watched until the nest has been found. By regularly checking the nest to ascertain whether it has been abandoned, more than one nest can be found in each territory. This nest searching was carried out on 20 separate days between 3rd April and 15th June 1990 (dates given in table 5.1, being the same days as observations were made on chaffinch behaviour), an average of 4 hours per day. In this manner a total of 80 hours in a search covering 120 hectares, which included careful searching of 10 identified territories, revealed 5 nests, only 3 of which were still intact and so collectible, by the end of the breeding season.

By these 4 means, a total of 38 nests were collected, and examined as described below.

The information about where and when these nests were found is given in appendix A, which also indicates the materials present in each nest. The numbering of nests as given in this table is used throughout this thesis.

5.3.2) Examination of the materials in each nest

For the purposes of this study, it is convenient to divide the layers of the nest slightly differently from those described by van Dobben (1949) and Marler (1956) (figure 2.1). I identify (A) the Superficial layer, (B) Foundation layer plus rim, (C) Inner layer, and (D) Lining. This only differs from the scheme of the earlier authors in having the rim included with the Foundation layer rather than the inner layer. This may not reflect the mode of construction of the nest, but it separates the layers visible from the outside (A and B) from those that are not (C and D). This scheme is therefore more relevant to the functioning of the nest.

The materials used in each nest and visible from the outside, were listed in order of abundance, by volume rather than numbers. Where the number of pieces of a material could realistically be counted, they were. This applied to such materials as lichen or bark. The lining materials were not described, but the lining was checked for the presence of silk.

Those nests not from museums were dismantled to reveal the structure of the inner layer of moss and grass, and the materials included. The Lining (D) is easily lifted away from the Inner layer (C), since there is little material connecting the two parts. Likewise, the Foundation layer and rim (B), together with the Superficial layer (A), can be peeled away from the Inner layer. Hence the materials present in the distinct layer C can be examined.

5.3.3) Silk content and use in the nests

A 'unit' of silk was defined as a discrete piece of silk (web, retreat or cocoon) placed in the nest by the chaffinch. Retreats were hard to distinguish after they had been manipulated by the bird, and were probably frequently noted as webs. This is thus a possible source of error in the data collection and will be discussed later. Cocoons were easily distinguished on account of their structure or the regularity of the threads from which they are constructed.

The materials attached to each silk unit were recorded, together with whether the silk was in the Superficial layer (A) or embedded in the Foundation layer (B). Two special terms were used here. 'Embedded' means the unit was embedded as one compact unit in the Foundation layer and is opposed to 'stretched through' which is again in the foundation layer, but is applied to a unit that appears to have been pulled so that no core of silk is obvious. The distinction here is inevitably subjective, but probably real in terms of the function of the silk units concerned.

Those nests not from museums, and hence dismantled, were also examined for silk in the Inner layer (C), and the materials attached to any units were noted in the same way as for the outer layers.

The Lining (layer D) of those nests that possessed one were again examined for silk, and the number of units noted.

In this way, every unit of silk in the nest was recorded. Units of silk were taken from some of the nests for later attempts at identification (see below).

5.4) SILK IDENTIFICATION

5.4.1) Characterisation of silk from spiders at Garscube Estate

In order to attempt to identify silk taken from nests, a library was built up of silk from known spider species. Spiders were collected from Garscube Estate, together with the web, retreat and/or cocoon that each had spun. The spiders were killed in ether and preserved in 70% alcohol. They were subsequently identified (using Locket and Millidge 1951 and 1953, and nomenclature from Jones 1983). This produced a list of spiders, together with date of collection and location of each, found at Garscube Estate between the period October 1989 to June 1990. The list is not intended to include all the spiders present at Garscube, but should include all those species whose silken structures can be spotted and removed by small birds, by virtue of the fact that I could spot and remove them.

The silk collected with these spiders was examined. The first stage of the examination was a general description of each of the silk units obtained from the wild, spun by a known spider, under low (x6 objective) and high (x50 objective) power with a binocular microscope (x10 eye pieces). This description included colour, the number of different thread thicknesses visible, and any patchiness in the distribution of the threads. For cocoons and retreats, the overall structure was described using the binocular microscope.

Part of each sample was then prepared for examination under the Scanning Electron Microscope (SEM). They were mounted on stubs with double-sided sticky tape and sputter-coated with gold, at a thickness of 75nm, a treatment similar to that used by Craig (1987). Friedrich and Langer (1969) compared unfixed silk specimens and specimens coated with osmium, and found no difference in appearance between them, nor between specimens coated with different thicknesses of osmium.

Micrographs were taken at low power (x200 - x800) and individual threads were photographed at high magnification (x6400). At this magnification, the surface detail of the coarser threads is discernible, and the fine cribellar fibres of cribellate webs visible. A scale bar enabled fibre diameters to be accurately measured. Since electron microscopy is conducted under vacuum, humidity is low and constant. The temperature was also reasonably constant for all samples. These two environmental conditions affect fibre diameter (Work 1977, and see section 3.4.1), but since they are held constant in this study, variation due to them can be discounted.

Thus, in addition to those features noted under binocular light microscopy, the surface detail of the coarsest threads in each sample were described, and the diameter of the finest and coarsest threads was noted. From the electron-micrographs, the proportion of the various web-types present could be determined. The micrographs also provided a permanent record of the details of the silk unit.

5.4.2) Identification of unknown silk taken from nests

By treating silk units removed from chaffinch nests in precisely the same manner, they could be compared with known spider silk, in order that attempts could be made to identify as far as possible the unknown silk unit. The following details were compared on a checklist of qualitative descriptions of the silk units: silk colour(s); homogeneity of structure; the presence of single-layered sheets of silk; anastomosis of silk threads; the presence of exceptionally coiled or exceptionally straight threads; the presence of loose or tight bundles of fibres; and the surface detail of the coarser fibres. Quantitative measures were also taken: the number of different diameters of silk fibres; and the diameters of the coarsest and finest fibres. Finally, where these properties show close similarity between the unknown silk and one or more known units, electron micrographs, and parts of the original samples if available, could be directly compared visually, and a tentative decision as to identity to at least family proposed.

Most of the unknown silk units involved were taken from nests found in 1989 and 1990 at Garscube Estate, since the types of silk present for a range of spider species in this area are known and described. Units were chosen as a representative of the types of silk present in the nest. Upon examination of a particular nest, silk samples were taken so that for each set of materials to which the silk is attached, all types of cocoon and web that could be discerned as different were taken. For example, all the different webs and all the different cocoons that were attached to lichen and moss were taken for closer examination. At this stage, units were classified as different if they did not appear identical under the binocular microscope. Subsequently, where two or more silk samples taken from one nest, but attached to a different set of materials, appeared identical under the binocular microscope, only one was examined and described, using the checklist above, under the SEM.

5.5) SILK AVAILABILITY

5.5.1) Year-round survey of webs, retreats and cocoons

The relative availabilities of spider silks during the nest-building period will affect the relative amount of the silks in chaffinches' nests. In order to assess the availability of a wide range of silk types from a wide range of species present in the study site, a cross-section of habitats within Garscube Estate, which would be accessible to birds for collection of nesting material, were chosen. The total numbers of webs, retreats and cocoons visible at these sites were counted. This method was used since accurately sampling spider populations, as with other invertebrates, is notoriously difficult (see Turnbull, 1973, for a review of the use of various methods), and in any case it is the number of visible silken structures that is important in this study, rather than numbers of

spiders *per se*. The sites used are listed in table 5.2, and located on the map in figure 5.1. Figures 5.2 (a-h) are photographs of these sites. They include both man-made structures and natural vegetation.

Counts were carried out throughout the year (dates shown in table 5.3), on average once a fortnight, but more frequently during the breeding season (around weekly between April 16th and July 4th), and less frequently (about monthly) during the summer (July 19th to September 26th) and winter (December 13th to February 2nd), when little change in the numbers of active spiders occurs (Turnbull 1973).

The type of web was recorded as belonging to one of five categories: (i) cribellate sheet (Amaurobiidae); (ii) ecribellate sheet (Agelenidae, Linyphiidae); (iii) orb (Araneidae, Metidae); (iv) irregular (Theridiidae); or, if the web was in such a bad condition that it could not be identified with certainty, it was recorded as (v) 'Cob Web'. These were the only web-building families represented in the sites observed. Non-web building families will have been present in large numbers in the area, but not recorded in this manner. However, the cocoons of some of these families (see Silken Structures, above) would be available to the birds, and hence were recorded.

The classification to family of cocoons and retreats is not possible in a manner akin to that for webs due to the great variability between species, so was not attempted. However, it was sometimes obvious, where the cocoon or retreat was close to a web, which spider was responsible for it. In these cases, the spider was collected and identified.

Hence, on the score sheet, 7 categories of silk available to birds were recorded - 5 web types, retreats and cocoons - from the 8 sites (table 5.2). The number of each silk type was recorded for each site separately on each observation day.

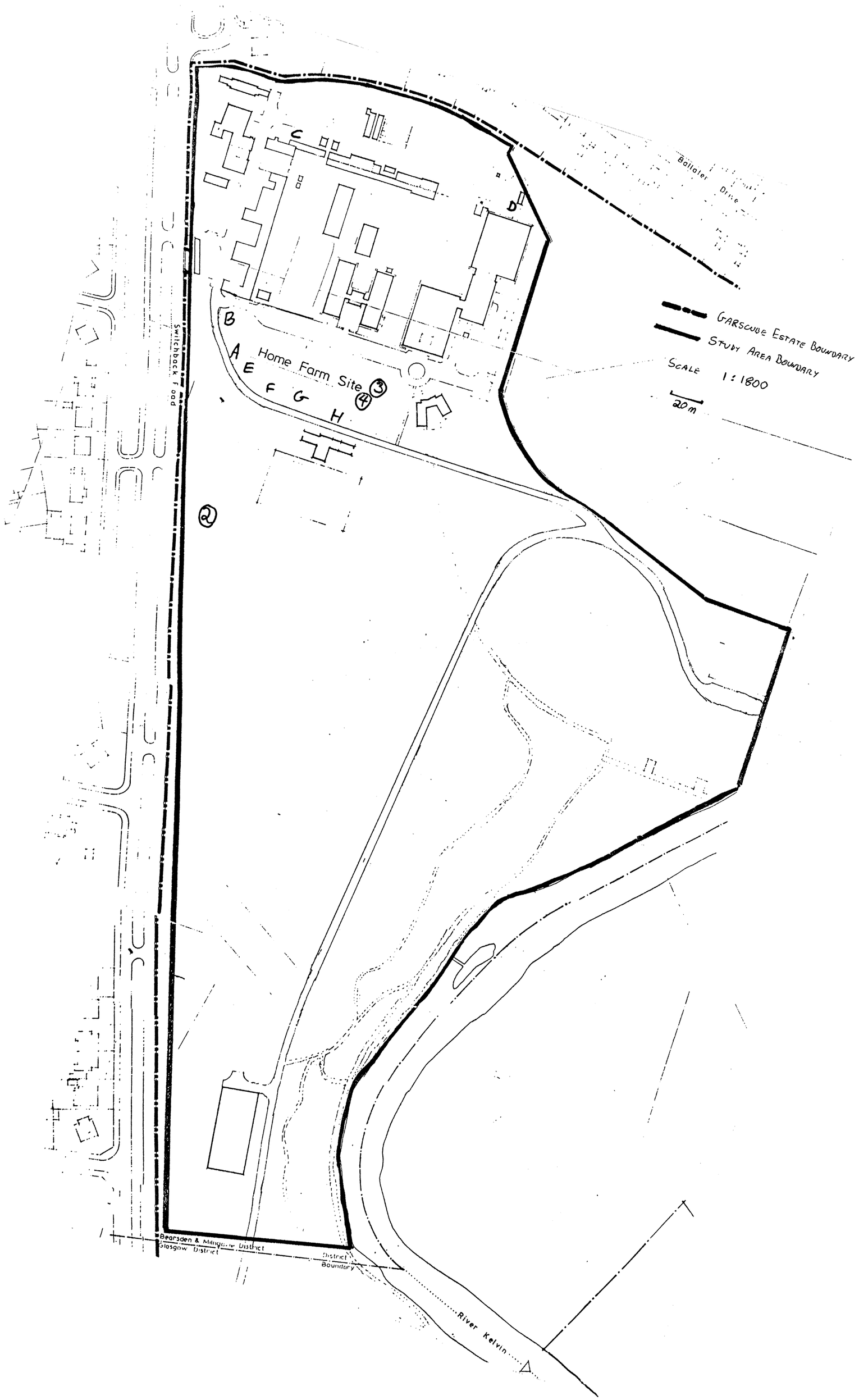
Ballater Drive
Switchback Road
C
D
B
A
E
F
G
H
Home Farm Site
4
3
2
GARSCUBE ESTATE BOUNDARY
STUDY AREA BOUNDARY
SCALE 1:1800
20m
Bearsden & Milngavie District
Glasgow District
District Boundary
River Kelvin

Table 5.2 The sites at Garscube used for the year-round survey of spiders' webs retreats and cocoons. Also shown, in the last column, is the figure number of the photograph showing the site. The letter codes given in column 1 locate each site on the map in figure 5.1.

Code	Site	Figure
A	Holly hedge, one side	5.2(a)
B	Sign post	5.2(b)
C	Carport, two sides	5.2(c)
D	Bicycle shed, outside wall	5.2(d)
E	Gean tree (1), lower 6 feet	5.2(e)
F	Gean tree (2), lower 6 feet	5.2(f)
G	Beech tree, lower 6 feet	5.2(g)
H	Yew tree, lower 6 fet	5.2(h)

Figure 5.1 Map of Garscube Estate. The thick solid line delineates the boundary of the area covered by the search for chaffinch nests and spiders. The eight sites marked A - H, listed below, are those described in table 5.2, and shown in figure 5.2, where the spider silk survey was carried out. The numbers 2-4 are where Nests 2 - 4 were found.

Code	Site
A	Holly hedge, one side
B	Sign post
C	Carport, two sides
D	Bicycle shed, outside wall
E	Gean tree (1), lower 6 feet
F	Gean tree (2), lower 6 feet
G	Beech tree, lower 6 feet
H	Yew tree, lower 6 fet

Figure 5.2 (A) Holly Hedge.

Figure 5.2 (B) Sign Post.

Figure 5.2 (C) Car Port

Figure 5.2 (D) Bicycle Shed

Figure 5.2 (E) Gean Tree (1).

Figure 5.2 (F) Gean Tree (2).

Figure 5.2 (G) Beech Tree.

Figure 5.2 (H) Yew Tree.

Table 5.3 Dates when the silk counts were made for the year round survey of web, retreat and cocoon numbers at the sites given in table 5.2, Garscube Estate.

November 1989:	May 1990:
15th, 30th	3rd, 11th, 18th, 24th
December 1989:	June 1990:
13th	1st, 8th, 14th, 21st, 28th
January 1990:	July 1990:
10th	6th, 19th,
February 1990:	August 1990:
5th, 22nd	22nd
March 1990:	September 1990:
7th, 21st	26th
April 1990:	October 1990:
3rd, 16th, 27th	11th, 23rd

5.5.1.1) Effect of time of day on silk count.

There is a potential problem that the time of day that the count was made could affect the number of webs counted. There are two possible reasons for this. The light conditions vary during the day, and so may the make visibility of webs change. Also, orb webs which are replaced daily may not be present at all times of the day, their presence being dependent upon the spiders' circadian rhythms. To compensate for this, counts were made in both the morning and afternoon on the four occasions between 28th June and 22nd August inclusive. Since no regular or large differences showed up (see section 6.4.2.3), the time-consuming second count was abandoned. The time-of-day of the count was varied through the year.

5.5.2) Investigation of the turnover of retreats and cocoons

In order to see specific cocoons or retreats disappearing during the bird breeding season, it was necessary to monitor the silken structures in a specific area. From January 10th 1990 until August 23rd 1990, the positions of spider retreats and cocoons attached to the ceiling and rafters inside the bike-shed (the outside wall of which is site D, table 5.2) were mapped on the same dates as the web counts (table 5.3). The ceiling is divided by rafters into rectangles of 75 by 90 cm. Four of these were drawn and the position of each cocoon or retreat marked. Hence, the dates of appearances and disappearances for individual, specific structures could be ascertained. The dates of hatching of cocoons was also noted.

CHAPTER 6

RESULTS

6.1) TIMING OF CHAFFINCH BREEDING AT GARSCUBE ESTATE

Ten occupied chaffinch territories were identified at Garscube Estate in 1990. The timing of nest-building in these territories is the important stage of the breeding cycle for this study. If this is known, the relative amount of silk available to the chaffinches as a nesting material is also known, from the study of web, retreat and cocoon numbers throughout the year autumn 1989 to autumn 1990. Since nest building was rarely witnessed, the following is a chronological account of the various reproduction-related behaviours observed at Garscube. From the timing of these behaviours, the timing of nest-building can be estimated by extrapolation, using information about the duration of stages in the breeding cycle given by Newton (1964).

Reproduction-related behaviour was first observed on 16th April, though it may well have been occurring earlier in the spring. This first record consisted of one male singing against another from a neighbouring territory, in the presence of a female. Hence, by this time, it is clear that territories had already been established, and courting had begun. On 24th April, two males were seen fighting.

On 25th April, one female appeared to be examining potential nest sites, in the manner described by Marler (1956). By April 30th, the nest of a different female was found, near completion, in a rhododendron bush. She was observed collecting materials and placing them in the lining of the nest. On 4th May, a second nest was observed high in a yew tree,

only visible from a distance. It appeared, through 8x30 binoculars, to be at or near completion, since the Superficial Layer was extensive. Both of these nests had been destroyed by 11th May.

Copulation was observed only once during the season, on 3rd May, occurring between the female that had been seen examining nest sites earlier, and her mate. Solicited copulation occurs towards the end of the nest-building phase and during egg-laying (see section 2.4).

A third nest (Nest 4) was discovered on 7th May, 12 feet high in the outer branches of a yew tree, in a small area of land with scattered mixed trees and bushes. Again, the nest appeared to be near completion. One visit by the female was observed on this day. The nest was subsequently abandoned. Upon collection, I discovered that the lining was complete, but no eggs had apparently been laid in it.

On 11th May, a fourth nest (Nest 2) was discovered, partially built. It was in a small young beech tree, about 6 feet above the ground, in the angle made by a lower branch with the trunk. The female was in the nest, while the male, perched nearby, emitted a warning call. This nest had been abandoned and partly destroyed a week later, and was collected on 22nd May. No replacement nest built by this pair was found at Garscube Estate.

On 5th June, a previously unobserved pair of chaffinches was seen feeding and collecting food, but after careful attempts at tracking the adults in a region of dense mixed woodland, no nest was found, and no young were discovered. On 10th June, newly-fledged young in another territory were discovered, well hidden in undergrowth, being fed by their parents.

Nest 3 was discovered 8 feet above the ground, in the upper branches of a small

rhododendron tree, neighbouring the yew tree of Nest 4. It was discovered and collected on 15th June, signs of predation being evident - the lining was scattered amongst nearby branches and there was a neat hole in the side wall of the nest.

By 28th June, all male chaffinch singing had ceased, but feeding of young was observed until 6th July.

This timetable of chaffinch breeding at Garscube Estate in 1990 agrees closely with that described earlier for the whole of Great Britain (after Newton 1964). My observations can be summarised as follows. Courting occurred during April, with nest-site examination being seen during the second half of the month. Judging by the state of completion of nests found, nest-building occurred during the last days of April and up to mid-May, with a female seen soliciting copulations in early May. This is, as expected, a few days later than the normal for Britain as a whole. Food collection for nestlings and fledglings was observed during early and mid-June. The last reproductive behaviour - the feeding of large fledglings - was observed in early July.

The whole season appears to have taken rather shorter than might be expected from the data given by Newton (1964) for northern Britain (section 2.4.1). It started later than, but finished at the same time as, the average for Britain, as given by Newton (1964). This can be attributed to a rather warm spring of 1990 - a hot spell started at the end of April and lasted almost continuously for a month. This may have resulted in an abundance of defoliating caterpillars allowing the young to be fed and to grow at a faster rate than usual.

6.2) INVESTIGATION OF CHAFFINCH NESTS

6.2.1) Nest dimensions

Nest size varied between an average diameter of 82.5mm and 102.5mm in those nests that had not been partially destroyed or badly squashed. The mean was 95.56mm, with a standard deviation of 5.20, from a sample size of 27 nests.

6.2.2) Investigation of the materials in each nest

Appendix A gives a check-list of the materials found in Layers A (Superficial) and B (Foundation/Rim) of each nest. Where the number of pieces of a material was counted, this value is given in the table in parentheses.

The 38 nests show a great diversity of composition, but the structures of all but one are composed primarily of moss (the remaining one is primarily built from rootlets and cotton wool). This variety of composition reflects the variety of habitats in which the nests were built, a feature of chaffinch biology that contributes to its current success as a breeding bird in Britain. In total, 21 nesting materials were found in the outer layers (layers A and B). These are listed in table 6.1, which also gives the number of nests in which each material was found. In this table, and elsewhere in this thesis, the term 'wool' refers both to animal wool and man-made cotton-wool, these sharing properties which make them similar nesting-materials. The term does not include natural plant fibres, such as plant-down, which are given there own categories, since the properties are more divergent. Some of the materials, such as leaves and feathers, may not have been placed in the nest deliberately, but become attached to the outside by accident. It can easily be envisaged that they have fallen onto the nest by some means, or been wind-blown, after completion.

Table 6.1 Materials found in Layers A and B of chaffinch nests, showing the number of nests in which each material was found, placed in order of frequency of occurrence. In parentheses are the percentage of nests that contained each material.

Material	Number (and %) of nests using the material
Moss	38 (100%)
Silk	35 (92%)
Twigs	34 (89%)
Wool	30 (79%)
Grass	29 (76%)
Lichen	26 (68%)
Bark	21 (55%)
Feathers	21 (55%)
Hair	12 (32%)
Rootlets	12 (32%)
Leaves	9 (24%)
Paper/Tissue	7 (18%)
Wood Strips	7 (18%)
Plant Down	6 (16%)
Seeds	5 (13%)
Wood Chips etc	5 (13%)
Woody Fibre	3 (8%)
Pine Needles etc	3 (8%)
Fabric	2 (5%)
String	2 (5%)
Animal Skin	1 (3%)
Number of Nests	38

The largest number of different materials counted in Layers A and B any one nest was 11 (in Nests 5 and 16). The smallest number was 5 (in Nests 35 and 37). The mean number of different materials per nest was 8.13, with a standard deviation of 1.51.

The most common nesting materials for Layers A and B, present in almost all the nests examined, are moss, grass, twigs and silk, with wool and lichen also found frequently. Since the nests are built around or on twigs and branches, it is inevitable that twigs will present in a high proportion of nests. However, several nests also have fine twigs attached to the outside and woven through the foundation and these twigs do not appear to form part of the base. Wool (including cotton wool) can form a major part of Layer B, sometimes almost as abundant as the moss, but more usually, it is found pressed into the outside of the nest. Lichen is usually used as part of Layer A, but occasionally, this material is found pushed well into the moss structure.

Other materials can be used in similar situations to the common ones described above. For instance, in many cases, rootlets form a major part of the nest structure, as can, more rarely, long strips of bark and wood (Nests 11, 17, 34 and 35) and other woody fibres (Nests 3 and 4). In some nests, animal hair is woven into the nest in a similar manner to grass. It is noticeable that those nests with much hair (nests 5, 14, 15, 32 and 38) tend to have little or no grass content. It is not the case that these nests were in any worse a state of repair than others, so the hair is not part of the Layer D (Lining) that has become mixed with Layer B (Foundation) or C (Inner). This possible relationship between grass and hair will be discussed again later.

Materials like bark, wood chippings, and paper also appear in the Layer A of some nests.

6.2.2.1) Nests built by the same female.

Nests 3 and 4 from Garscube Estate were probably built by the one female in

neighbouring trees, about 20 metres apart, in the 1990 season. Unfortunately, no chaffinch visits to Nest 3 were witnessed, so the supposition, based upon the nests' proximity, is unconfirmed. Nests 8 and 9 were both found close together in 1989 in an ivy bush, and were probably both built by the one female. Similarities and differences between nests built by the same female can indicate how much the habitat composition may influence the nest composition (see section 7.1).

6.2.2.2) Effects of timing of nest-building.

The dates of construction of the nests, as well as the habitat-type, will affect the range of materials available for the nests. Unfortunately, this information is lacking in nearly all cases except for the three I found at Garscube Estate in 1990 (Nests 2 - 4). Nests 2 and 3 were discovered on the same day (11/5/90), with Nest 3 more-or-less complete, but Nest 2 only having Layers B and C complete, with Layer A hardly noticeable. Nest 2 was abandoned soon after my discovering it, with the Layer A closer to completion, but no Layer D (lining). Nest 4 was found some weeks later, completed, but it had been predated and partially destroyed, predator unknown.

6.2.3) The silk content of nests

Silk was looked for in the four Layers A (Superficial), B (Foundation/ rim), C (Inner) and D (Lining), working from the outside inwards.

6.2.3.1) Distribution of silk through the nest.

Table 6.2 gives the number of units of silk found in the two outer Layers A and B combined, Layer C, and Layer D, and the number of nests with silk in these Layers, together with a breakdown in terms of type of silk unit (web, cocoon or retreat). A total of 1581 silk units were found in Layers A and B of 38 nests examined, and 44 in Layer C of 20 nests (those that were not from museums and were in good enough condition to identify the layer as distinct). In all these layers, web and cocoon silk units were found in

Table 6.2 Breakdown of silk types (webs, retreats and cocoons) present in Layers A, B and C of chaffinch nests. No units of any silk type were found in Layer D.

LAYERS A & B

	No. of Nests with one or more Units	Number of Units	Mean no. of Units/Nest	Standard deviation
Web	27	468	12.3	15.10
Cocoon	33	1089	28.7	40.65
Retreat	9	17	0.4	0.94
Unidentified	4	7	-	-
Total Silk	35	1581	41.6	42.18
Number of nests Examined	38			

LAYER C

	No. of Nests with one or more Units	Number of Units	Mean no. of Units/Nest	Standard deviation
Web	4	9	0.4	1.02
Cocoon	11	27	1.3	1.98
Retreat	6	7	0.3	0.57
Unidentified	1	1	-	-
Total Silk	13	44	2.2	2.79
Number of nests Examined	20			

far higher numbers than retreat silk. No silk was found in Layer D of any of the nests with this layer intact.

There is a large variation in the number of silk units in the combined Layers A and B of a chaffinch nest. Three nests lack silk completely, several nests have fewer than ten units, while three have more than 100 units, the highest being 196 (nest 14).

6.2.3.2) Effect of nest size upon number of silk units

The Kruskall-Wallis test was used to determine whether there is any significant effect of nest size upon number of silk units. Three size classes of nest were used - small (up to and including 90mm diameter), medium (92.5 to 97.5mm diameter) and large (100mm diameter and larger). No significant differences were found between the three classes in total silk content (KW = 0.61, N = 27), nor were there differences in the amount of silk embedded in Layer B of nests in the three size classes (KW = 0.19, N = 27).

6.2.3.3) Materials to which silk is attached.

How the silk in Layers A and B is distributed between the various materials it is attached to is summarised in table 6.3. Some of the silk units are attached to more than one type of material, and so are counted more than once in these calculations. In particular, silk embedded in Layer B can also be attached to materials in Layer A. This is why the silk for the two layers have been included in the same table, and summary statistics are given for the two layers combined.

The only roles possible for silk in Layer C are holding the nest's moss, grass and rootlet structure together, and occasionally attaching the nest to the twigs that support it. Both of these uses were found, and no other materials were involved, apart from occasional pieces of lichen.

Table 6.3 Silk usage in Layers A and B of the 35 nests with silk. The first column gives the usage to which silk units are put, the second column gives the percentage of silk units put to each usage. The third column gives the number of nests that possess both silk and the material involved in each usage, though this number is not necessarily restricted to those nests exhibiting the usage.

The final column gives the mean and standard deviation of units put to each usage per nest that possesses both silk and the material.

Usage	% of All silk units	Number of Nests	Mean number of units/nest (s.d.)
Embedded in Foundation	36.5%	35	16.4 (15.7)
Attached to Lichen	31.2%	25	19.8 (28.0)
Attached to Bark/Wood	15.9%	29	8.6 (28.4)
Attached to Twigs	7.2%	30	3.8 (3.9)
Attached to Grass	6.0%	28	3.9 (9.1)
Other Uses	3.2%	-	-

6.2.3.4) Correlations between silk and other materials

The data used in the following paragraphs are summarised in Appendix A, which gives a checklist of materials present in each nest, together with the number of pieces of those materials that were counted.

Correlation coefficients, calculated using Spearman Rank Correlation (Siegel 1956) for the number of silk units against the number of those materials that were counted - lichen, bark/wood, twigs and wool - were examined. For the first three, Spearman's r was used on ranked data. The results are given in table 6.4. The only significant correlation is a positive one between number of silk units and number of pieces of lichen ($r_s = 0.488$, N = 38, significant at 5% level).

Table 6.4 also gives the correlation coefficients for ranked values of the number of units of silk attached to a type of material and the number of pieces of that material (only those nests that contained the material being investigated were included). Again, the only significant correlation is that with lichen, also positive ($r_s = 0.884$, N = 26, significant at 1% level). The Kruskall-Wallis test showed no significant effect of nest size , using the three size classes given in section 6.2.3.2, upon the number of pieces of lichen present (KW = 0.447, N = 27).

The situation with wool is more complicated. The numbers of pieces of wool per nest are small, and there are many ties between nests. So, nests were divided into five categories, according to how many pieces of wool they contained (none, 1 to 5, 6 to 10, more than 10, and nests where wool is a dominant structural material). The Jonckheere Trend test (see Siegel 1956) was used to look for correlations between the category of nest and the number of silk units per nest. No trend was found between number of pieces of wool and number of units of silk in a nest ($J^* = -0.709$, N = 38, $p > 0.1$).

Table 6.4 Spearman rank correlation coefficients (r_s). The second column gives the r_s for the number of silk units in a nest with the number of pieces of each of three materials - lichen, bark/wood and twigs. The third column gives the number of nests included in the test.

The fourth column gives the r_s for the number of silk units attached to each material with the number of pieces of the material. The nests involved in the test is restricted to those that possess the material. The number of nests is given in the final column.

	Correlation of number of Units with number of pieces of material		Correlation of number of Units attached to material with number of pieces of material	
Material	r_s	N	r_s	N
Lichen	0.488*	38	0.884**	26
Bark/wood	-0.005	38	0.316	31
Twigs	-0.146	38	0.251	33

* = significant at 5% level, ** = significant at 1% level

6.2.3.5) Silk distribution between the materials.

The chi-square test was used to examine whether silk is distributed evenly between three types of material - lichen, bark/wood and twigs. Expected numbers of silk were calculated using known proportions of the three material types. When data for all 38 nests were combined, twigs were found to have significantly more silk attached than predicted from the numbers of the materials present ($X^2 = 33.4$, df = 2, significant at 1% level). There is a problem of size here. Twigs range in size from less than 10mm long to over 100mm. Bark/wood includes material in strips of around 100mm in length, but mostly covers flat woody materials in the region of 5 x 5mm. The size of lichen pieces is in a similar range to the small woody materials. The differences in size mean that some twigs can have several silk units attached to them, while more than one wood chipping or piece of lichen can be attached to one silk unit. This point will be discussed again later.

6.2.3.6) Differences in the extent of the use of web and cocoon silk.

Differences were looked for in the uses to which web silk and cocoon silk are put. The Wilcoxon matched pairs test shows that the numbers of units of cocoon silk and the number of units of web silk per nest are different. The median for cocoons is significantly higher (5% significance level) than the median for webs ($Z_T = 1.998$, N = 35). Furthermore, There is no correlation between the number of web units in a nest and the number of cocoon units ($r_s = 0.049$, N = 38).

6.2.3.7) Correlations of web and cocoon with lichen, wood and bark.

The number of cocoons in a nest shows a positive correlation with the number of pieces of lichen ($r_s = 0.460$, N = 38, significant at 5% level), and the number of cocoons attached to lichen shows a positive correlation with the number of pieces of lichen ($r_s = 0.784$, N = 26, significant at 5% level), but web does not show a correlation in either parallel test ($r_s = 0.162$ and 0.333 respectively).

The Wilcoxon test on percentages of units attached to lichen showed no significant

differences between web and cocoon (T = 17, N = 12).

There is no correlation of either the number of cocoon units, or of the number of web units, attached to wood and bark with the number of wood and bark pieces (cocoons r_s = 0.121, webs r_s = 0.211, including correction for ties, N = 31).

6.2.3.8) Differences between web and cocoon in use in Layer B.

The Wilcoxon matched pairs test was used to see if there was a significant difference between the percentage of web units and the percentage of cocoon units that were found within layer B (combining 'embedded in' and 'stretched through' roles together). 12 nests were included in this test, these being the nests with more than five webs and more than 5 cocoons. This gave a T value of 12, which is significant at the 5% level, and indicates that more cocoons than webs are used in this manner.

When silk units 'embedded in' and silk units 'stretched through' Layer B are considered separately, again there is no significant difference in the percentage of cocoons used in each role and the percentage of webs used in each role, but there is a trend for a higher percentage of webs to be 'stretched through' (T_- = 4, N = 4) and a higher percentage of cocoons to be 'embedded in' (T_+ = 22, N = 12).

6.2.3.9) Comparison of wool with silk.

Finally, the role of wool is compared to the role of silk. It has already been noted that there is no correlation between the amount of silk and the amount of wool in a nest. Also there is no evidence that nests with a high web:cocoon ratio possess more wool than nests with a low web:cocoon ratio (Jonckheere test: J^* = 0.131, N = 35, 5 classes). Furthermore, there is no correlation between total cocoon silk and number of pieces of wool in a nest (Jonckheere test: J^* = -0.449, N = 38, 5 classes).

6.3) SPIDER SILK IDENTIFICATION

6.3.1) Characterisation of silk from Garscube spiders

6.3.1.1) The spider species whose silk was examined.

Fourteen species of spider were found at Garscube Estate, from 11 genera in 5 families (see section 6.4.1). Webs from only 10 of these species were collected and examined. Either the webs of the others contained too little silk to be examined, or no web was found near the spider. The species from which webs were examined are listed in table 6.5(a). Again due to low availability of silk with the spider nearby, cocoons from only three species were examined. These are listed in table 6.5(b). Both tables also give the number of each structure that were examined. I shall consider the characterisation of web and cocoon silk, using light and scanning-electron microscopy, separately. The characteristics thus obtained can be used to indicate to which species of spider the unknown silk units taken from chaffinch nests may belong.

6.3.1.2) Spider web characterisation.

Silk from *Amaurobius fenestralis* is easily distinguished by the presence of cribellar silk (diameter around 0.02 - 0.03μ), whose fibres are just discernible at the highest magnification used (x6400). Figures 6.1 - 6.5 are low and high magnification scanning electron micrographs of two different *Amaurobius* webs, showing cribellar puffs (as described in section 3.2.1) and coarser strands.

In order to demonstrate how clearly different these webs are from ecribellate webs, examples are given in the micrographs, shown in figures 6.6 - 6.9, of silk from webs of two species of Araneidae (*Araneus diadematus* and *Zygiella x-notata*) and in the micrographs in figures 6.10 - 6.13 showing silk from webs of two species of Linyphiidae (*Linyphia peltata* and *Stemonyphantes lineatus*). In these, there is a complete absence of the very fine fibrils characteristic of cribellar silk. Within each of the two families, distinctions between

Table 6.5 The spider species from which silk was collected at Garscube Estate and examined under light and scanning-electron microscopes - (a) web silk, (b) cocoon silk. The number in brackets after each species is the number of webs or cocoons from the species that were examined.

Table (a) - the webs

Species	(N)
THERIDIIDAE	
Steatoda bipunctata	(1)
Theridion varians	(1)
METIDAE	
Meta segmentata	(1)
ARANEIDAE	
Araneus diadematus	(3)
Zygiella x-notata	(3)
LINYPHIIDAE	
Stemonyphantes lineatus	(1)
Lepthyphantes sp	(1)
Linyphia montana	(1)
Linyphia peltata	(1)
AMAUROBIIDAE	
Amaurobius fenestralis	(9)

Table (b) - the cocoons

Species	(N)
THERIDIIDAE	
Steatoda bipunctata	(1)
ARANEIDAE	
Zygiella x-notata	(1)
AMAUROBIIDAE	
Amaurobius fenestralis	(1)

species are very unclear. Even between the families, no reliable differences can be seen; linyphiid silk tends to be more regular, consisting of fewer fibre-types, which are finer than the orb-web silk fibres. The maximum diameter of *L. peltata* web silk fibres found was 1.0μ (and no other linyphiid produced coarser silk), while that for *Z. x-notata* was 1.9μ, and for *A. diadematus*, 2.0μ. Araneid webs contain a few bundles of the coarser fibres (see, for example, figure 6.9), which presumably make up the frame of the web, whereas in Linyphiid webs, the fibres are less closely associated. Although pairs and bundles of fibres are frequent, these only exist for part of the length of the fibres involved, which frequently diverge. This is shown clearly in figure 6.10. It is this that produces the irregular meshwork of fibres that make up the sheet web. The surface details of the fibres involved are irregular, but inconsistent within families, and there appears to be overlap between the two in the extent of the ridges and bumps (compare figure 6.7, *Araneus* web, with figure 6.11, *Linyphia* silk, which both show more relief than figure 6.9, *Zygiella* silk).

Other characteristics of web silk looked at in attempting to spot patterns within relate species, and differences from other groups included the following: the presence of patches containing different types of silk, visible under the light microscope; the occurrence of anastomosis between silk fibres; the presence of tightly or loosely associated bundles of fibres; and the number of different silk diameters visible under SEM.

This process did not prove successful, partly due to the small numbers of webs found which had a spider clearly associated them, and the small number of species used, but also because these feature may not be reliable anyway. Fortunately, as we shall see in section 6.3.2.1, all the web silk found in nests contained cribellar fibrils, easily distinguished by the very fine diameter, and only one cribellate species was found at Garscube (*Amaurobius fenestralis*).

6.3.1.3) Spider cocoon characterisation.

Cocoons of only three species of spider were discovered - *Steatoda bipunctata*, *Zygiella*

x-notata and *Amaurobius fenestralis*. Of these, only for *Zygiella* was more than one specimen found.

Some basic distinguishing features between these three, discernible under SEM, are as follows:

The silk from *Zygiella* is very uniform, dominated by one fibre-type, single stranded and very coarse (4-6μ in diameter). Two or three finer fibre-types may also be present (the finest about half the diameter of the coarsest), but far more dispersed. The surface of the coarsest fibres consists of rough ridges running transversely, though the extent of this ridging appears to vary between individuals, as shown by the coarse silk taken from two different cocoons in the micrographs shown in figures 6.16 and 6.18. There is little structure within the cocoon, but the fibres are spun in a dense wool. Micrographs in figures 6.14 - 6.18 demonstrate these features. The colour of these cocoons ranges from yellow to golden brown. Three cocoons were examined.

The silk from *Steatoda* is also dominated by one fibre-type, but it is often present as a double strand, and sometimes in bundles of more strands. Again, occasional finer fibres are present. All the silk is far finer than that of *Zygiella*, the coarsest single strand being around 0.5μ. Micrographs in figures 6.19 - 6.21 demonstrate these features. The colour of this cocoon was dark grey. Only one cocoon was examined.

Cocoon silk from *Amaurobius* is far less regular in fibre diameter than the previous two species, since there is much anastomosis. Diameters in the sample collected range from 0.4 to 4μ. The cocoon structure is far more regular than the previous species, consisting of distinct sheets of anastomosing silk, with a few attaching threads. Micrographs in figures 6.22 - 6.25 demonstrate these features. The cocoon was white. Only one cocoon was examined.

The reliability of these features is impossible to assess with so few samples. However, they may provide indications as to which group of spiders the cocoons taken from nests may belong.

6.3.2) Examination of silk samples collected from nests

Silk samples were taken from Nests 1 - 4 (from Garscube Estate), Nest 29 (from a pear orchard in Oxfordshire, England) and Nest 33 (from Argyle, Scotland). For each nest, all the web and cocoon units that appeared to be different under the light microscope were then examined under the scanning-electron microscope to look for similarities with the silk from the known spider species collected at Garscube Estate, as given in table 6.5. The numbers of webs and cocoons examined from each nest are shown in table 6.6.

6.3.2.1) Web silk from nests

All the web silk units collected from the 5 nests that contained web silk, appeared to belong to cribellate spiders. Examples of silk from these units are shown as low power (x200-400) and high power (x6400) micrographs in figures 6.26 - 6.30. Fine cribellar fibres were present in all, and even intact cribellar puffs were found (e.g. figures 6.28 and 6.30). The appearance of each web unit was similar to that of the web silk spun by *Amaurobius fenestralis* at Garscube Estate, as described in section 6.3.1.2.

6.3.2.2) Cocoon silk from nests.

Some micrographs of cocoon silk taken from chaffinch nests are given in figures 6.31 - 6.36. Again, both low and high power micrographs are given. There is only rarely much resemblance between these and the known cocoon silks described in section 6.3.1.3. What similarities there are will be discussed in section 8.1.2.

Table 6.6 Number of web and cocoon units, of different appearances, removed for examination from 6 chaffinch nests. The location of the nests is also given. Nest numbering as in appendix A.

Nest	Number of Web units	Number of Cocoon units	Location
1	6	7	Garscube Estate
2	1	2	Garscube Estate
3	1	3	Garscube Estate
4	2	4	Garscube Estate
29	1	0	Oxfordshire, Orchard
33	0	1	Argyle, Open land

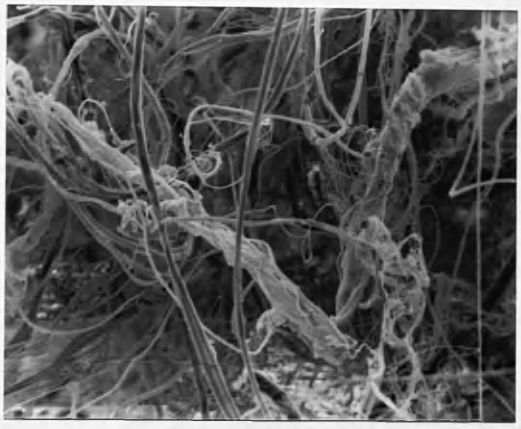

Figure 6.1: *Amaurobius fenestralis* male, web silk, low power (x400).

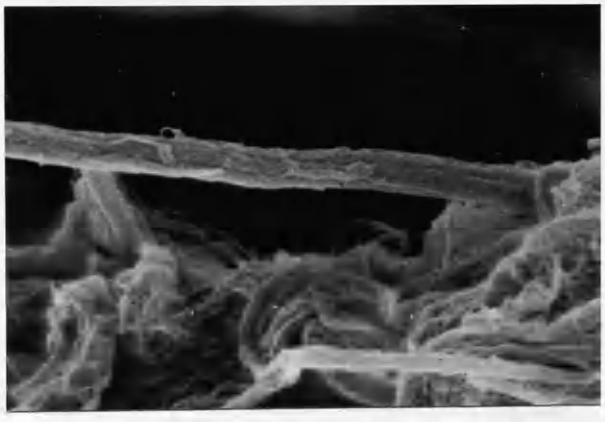

Figure 6.2: *A. fenestralis* male, web silk, high power showing cribellar puff and axial fibre (x4400).

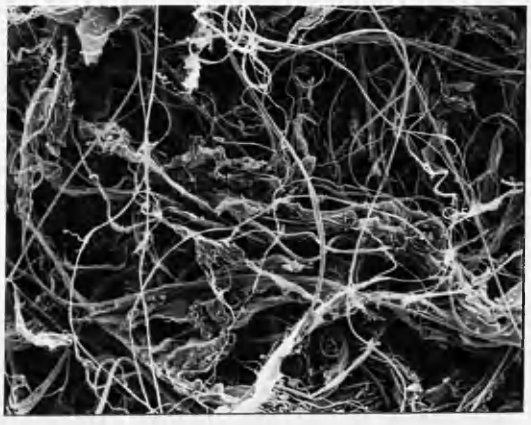

Figure 6.3: *A. fenestralis* juvenile, web silk, low power (x200).

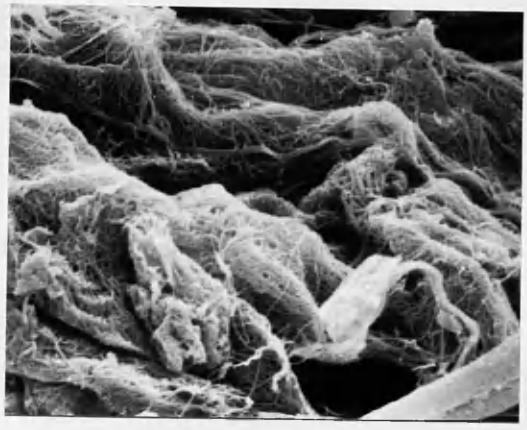

Figure 6.4: *A. fenestralis* juvenile, web silk, high power showing cribellar fibrils (x6400).

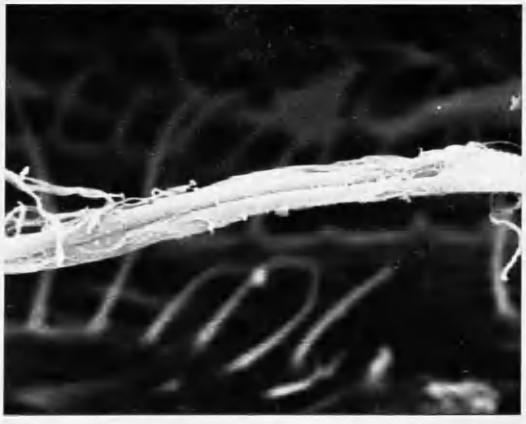

Figure 6.5: *A. fenestralis* juvenile, web silk, high power showing axial fibre pair covered with cribellar fibrils (x6400).

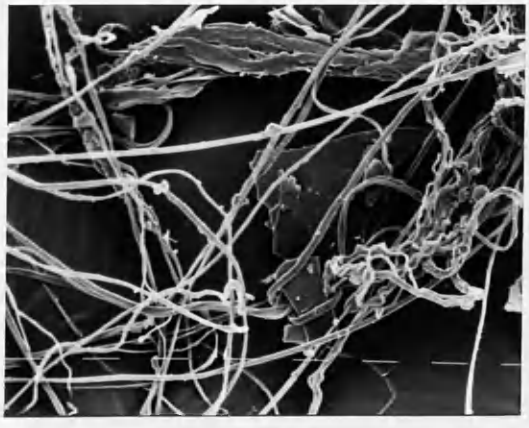

Figure 6.6: *Araneus diadematus* juvenile, web silk, low power (x800).

Figure 6.7: *A. diadematus* juvenile, web silk, high power showing three pairs of different fibre-types (x4500).

Figure 6.8: *Zygiella x-notata* juvenile, web silk, low power (x800).

Figure 6.9: *Z. x-notata* juvenile, web silk, high power showing bundle of fibres (frame thread?) (x6400).

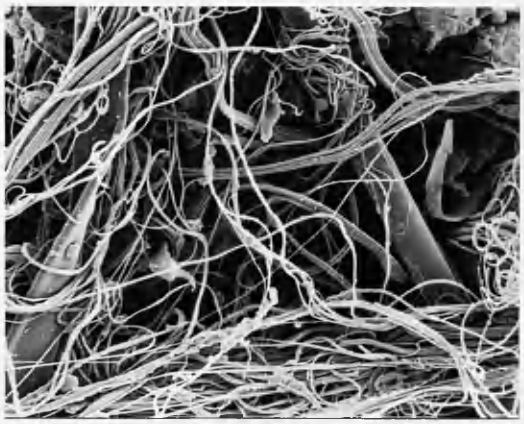

Figure 6.10: *Linyphia peltata* female, web silk, low power (x800).

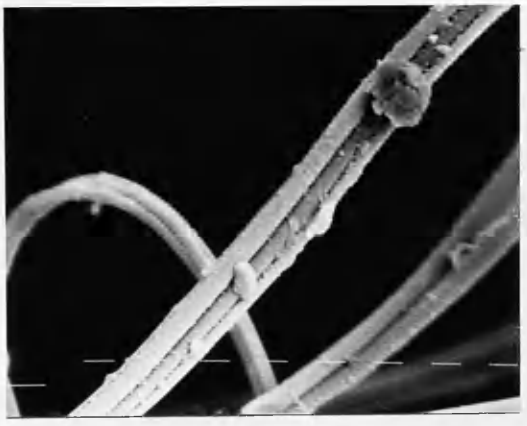

Figure 6.11: *L. peltata* female, web silk, high power showing small bundles of fibres (x6400).

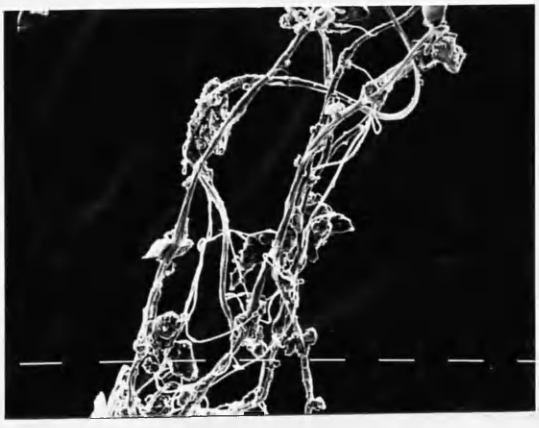

Figure 6.12: *Stemonyphantes lineatus* juvenile, web silk, low power (x800).

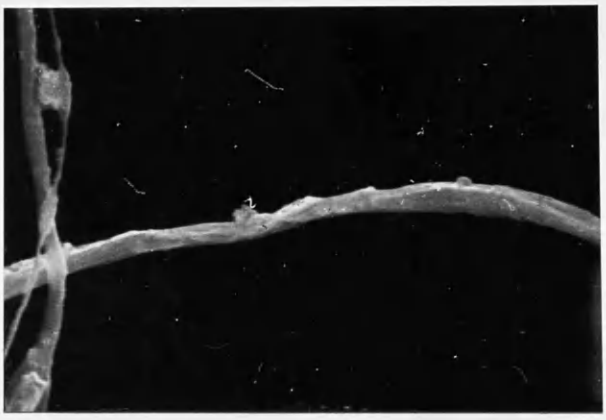

Figure 6.13: *S. lineatus* juvenile, web silk, high power showing the fine constituent fibres (x4400).

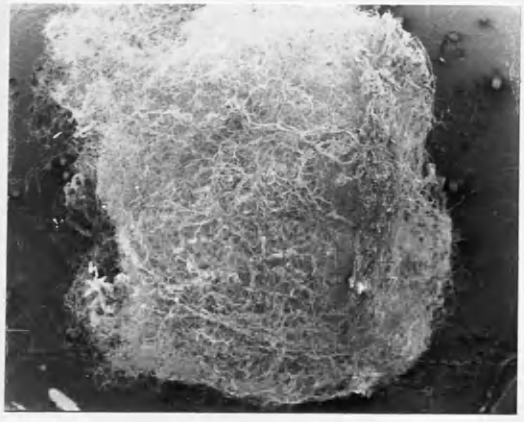

Figure 6.14: *Zygiella x-notata* cocoon, very low power to show different regions (x24).

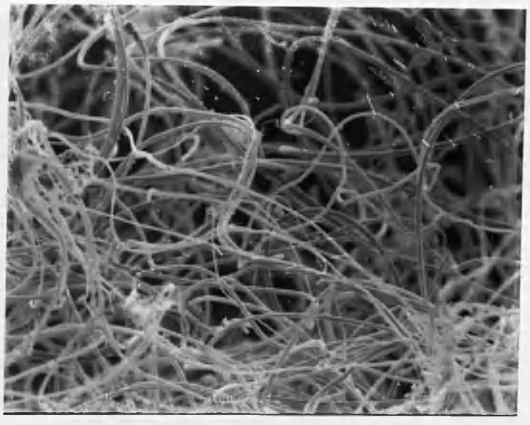

Figure 6.15: *Z. x-notata* cocoon, low power of typical region (x400).

Figure 6.16: *Z. x-notata* cocoon, high power to show surface of coarsest fibres (x6400).

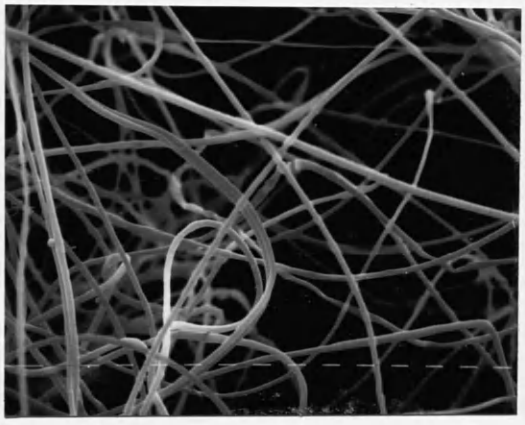

Figure 6.17: *Z. x-notata* cocoon, low power of second cocoon (x400).

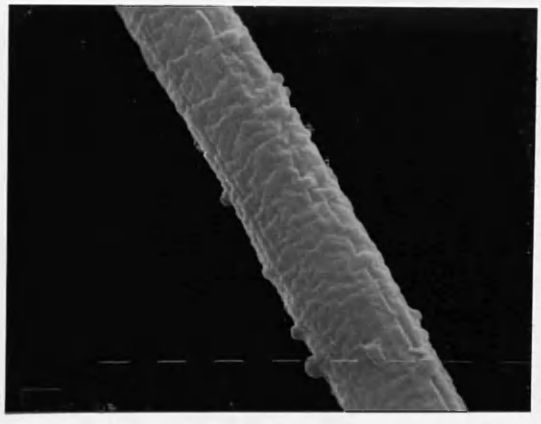

Figure 6.18: *Z. x-notata* cocoon, high power to show surface of coarsest fibre of second cocoon (x6400).

Figure 6.19: *Steatoda bipunctata* female, web silk, low power (x400).

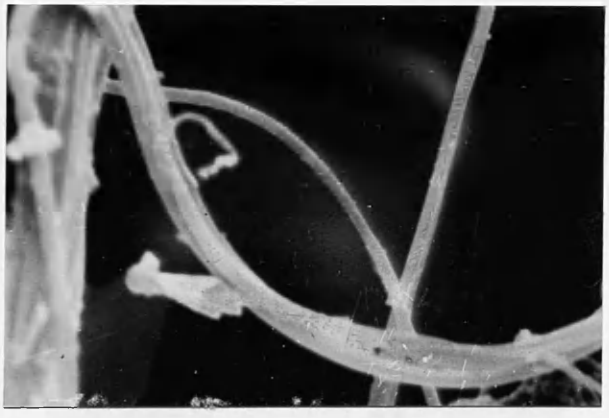

Figure 6.20: *S. bipunctata* cocoon, high power showing various fibres, some single, some double, some in larger bundles (x4500).

Figure 6.21: *S. bipunctata* cocoon, high power showing double thread with little surface detail (x4500).

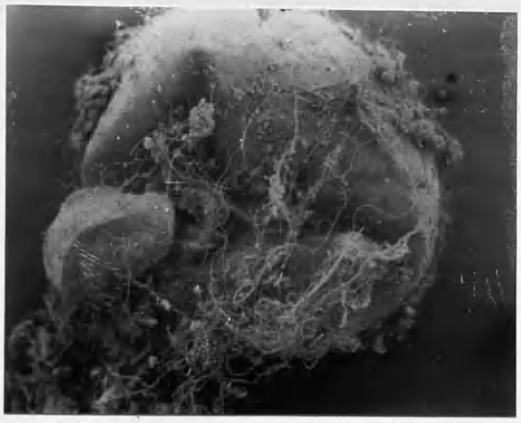

Figure 6.22: *Amaurobius fenestralis* cocoon, very low power to show attaching threads around layered egg sac (x24).

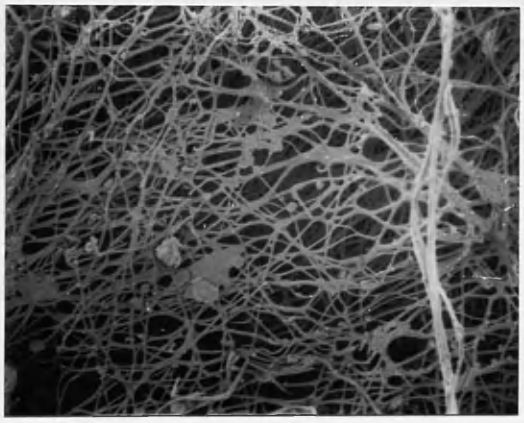

Figure 6.23: *A. fenestralis* cocoon, low power, showing separate layers of anastomosing silk (x400).

Figure 6.24: *A. fenestralis* cocoon high power of anastomising silk with little surface detail (x6400).

Figure 6.25: *A. fenestralis* cocoon, high power of attaching threads (x6400).

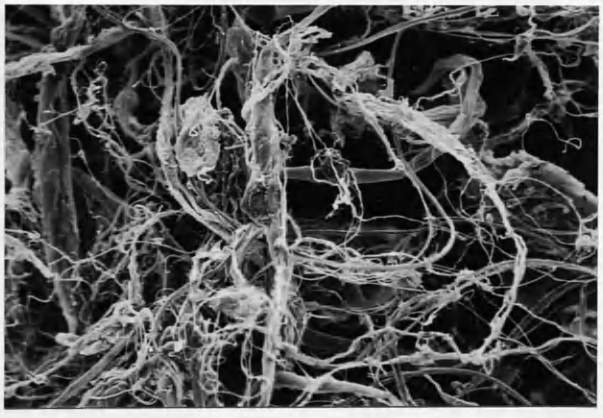

Figure 6.26: Sample L, web silk, from Nest 1, low power (x220).

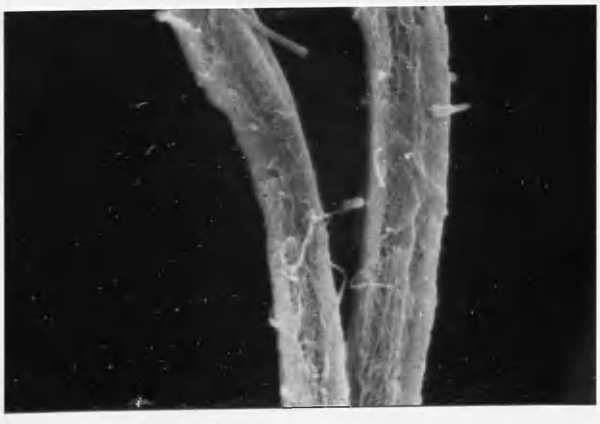

Figure 6.27: Sample L, web silk, from Nest 1, high power showing cribellar fibrils around axial threads (x4500).

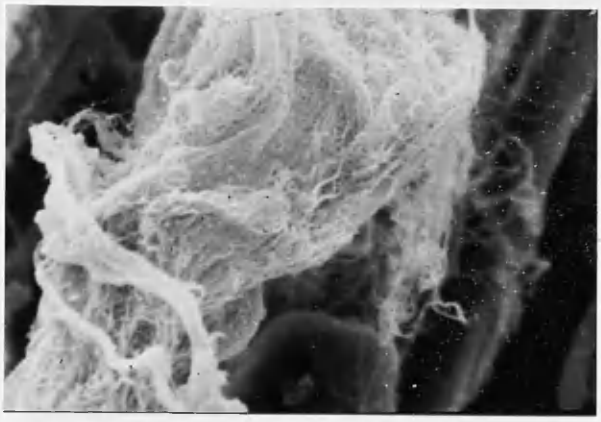

Figure 6.28: Sample of web silk from Nest 29, high power, showing intact cribellar puff (x4500).

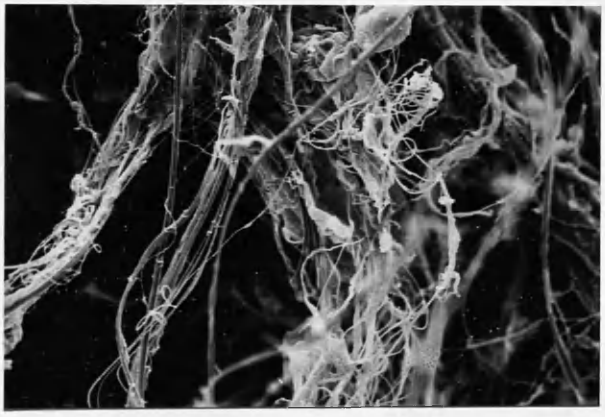

Figure 6.29: Sample N, web silk, from Nest 1, low power (x230).

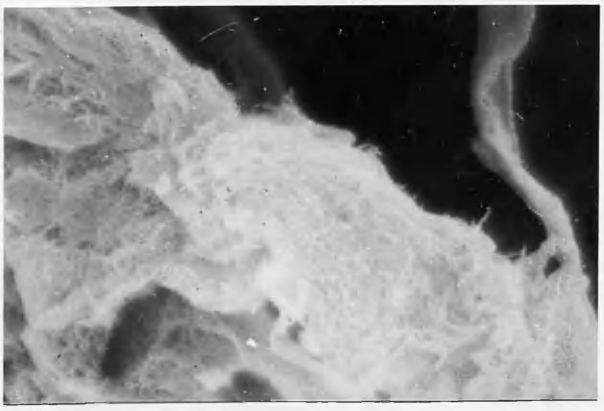

Figure 6.30: Sample N, web silk, from Nest 1, high power showing intact cribellar puff (x4500).

Figure 6.31: Sample I, cocoon silk, from Nest 1, low power (x200).

Figure 6.32: Sample I, cocoon silk, from Nest 1, high power, showing surface detail of coarsest fibre (x6400).

Figure 6.33: Sample A, cocoon silk, from Nest 1, medium power, showing several fibre types (x1600).

Figure 6.34: Sample V, cocoon silk, from Nest 1, low power (x200).

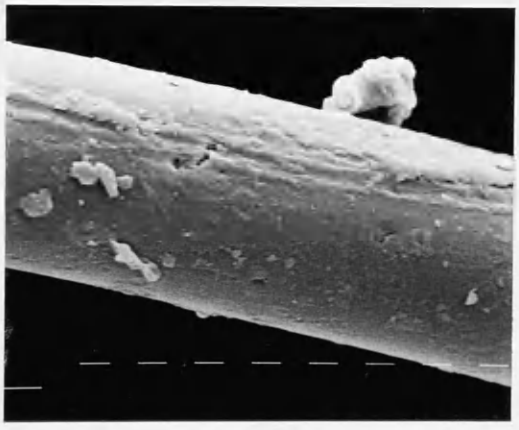

Figure 6.35: Sample V, cocoon silk, from Nest 1, high power showing surface of coarsest fibre (x6400).

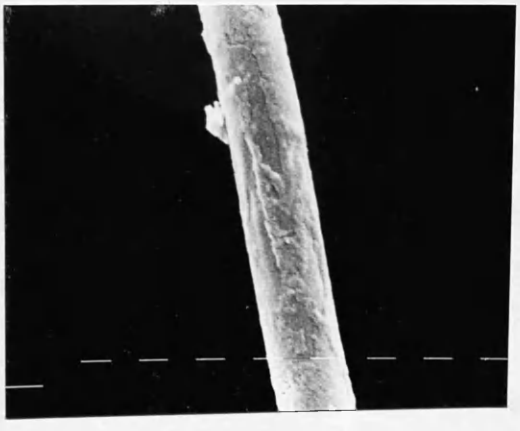

Figure 6.36: Sample V, cocoon silk, from Nest 1, high power showing surface of second coarsest fibre (x6400).

6.4) SILK AVAILABILITY

6.4.1) Spiders present at Garscube Estate

Fourteen species of web-building spider were found during the search of the sites used at Garscube, from 5 families. These are listed in table 6.7, together with the sex of the specimens found (or juvenile if immature), and the type of location where the species was typically found. This is not intended as a complete list of spiders present at Garscube, simply those whose webs were most visible and readily accessible to me, and by inference, to birds searching for nest materials. Appendix B contains a brief account of the ecology and life history of the species involved. The spiders found in greatest abundance were the following: *Amaurobius fenestralis*, *Zygiella x-notata* and *Meta segmentata* all year round, *Araneus diadematus* and *Lepthyphantes* sp juveniles in the autumn, and *Stemonyphantes lineatus* juveniles in the spring.

6.4.2) Year-round survey of webs, retreats and cocoons

6.4.2.1) Combined results from all sites examined

The results of the silk counts throughout the year November 1989 - October 1990, at the sites in Garscube Estate are shown in graphical form in figures 6.37 - 6.43. Dates are gien as day numbers, with 15th November 1989 as Day 1 and 23rd October 1990 as Day 344. Figure 6.37 shows how the total numbers of webs varied through the year, figure 6.38 shows the total number of retreats and figure 6.39 shows the total number of cocoons. Figures 6.40 - 6.43 give the breakdown for webs according to the four categories - cribellate sheet, ecribellate sheet, orb and irregular respectively.

There appears to be considerable random fluctuation in the number of silk units visible at the sites. The possible reasons for this are discussed later, in section 9.1.3. Figure 6.37

Table 6.7 List of web-building spiders found at Garscube Estate during the period October 1989 to June 1990, by family. Nomenclature follows that of Jones (1983). The second column shows whether females (f), males (e) or juveniles (J) were found. The final section gives information about where most of the specimens collected were found, with the site letter given in parentheses, where appropriate.

FAMILY and species	f, e or J	Where most specimens were found
THERIDIIDAE		
Steatoda bipunctata	f	Inside bicycle shed
Theridion varians	f	Outside wall of bicycle shed (D)
Theridion melanurum	e	Outside wall of bicycle shed (D)
Theridion pallens	J	Beech tree trunk (G)
METIDAE		
Meta segmentata	f,e	Holly hedge (A) and low vegetation
ARANEIDAE		
Araneus diadematus	J	Holly hedge (A)
Zygiella x-notata	f,e,J	Holly hedge (A), Carport (C)
LINYPHIIDAE		
Bathyphantes sp	J	Carport (C)
Stemonyphantes lineatus	J	Beech tree trunk (G)
Lepthyphantes sp	J	Holly hedge (A)
Linyphia montana	f	Holly hedge (A)
Linyphia peltata	f	Yew tree lower twigs
Microlinyphia impigra	f	Holly hedge (A)
AMAUROBIIDAE		
Amaurobius fenestralis	f,e,J	Bark of yew (H) and other trees, Carport (C)

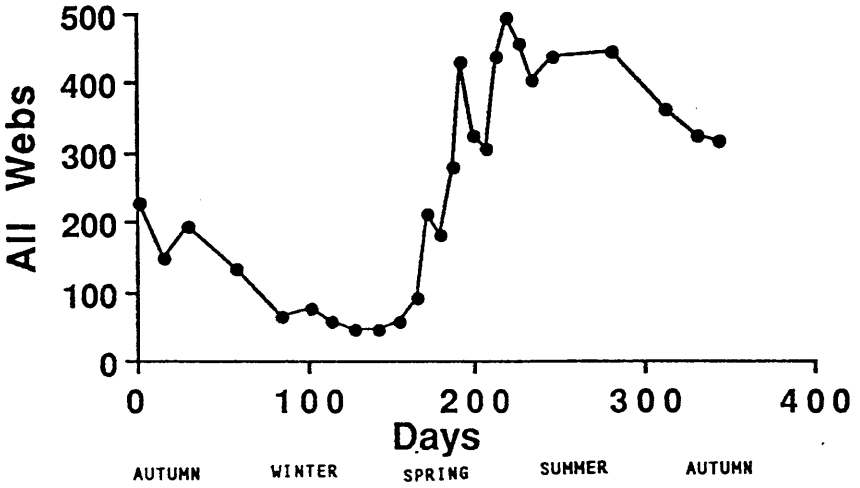

Figure 6.37 Total number of webs counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

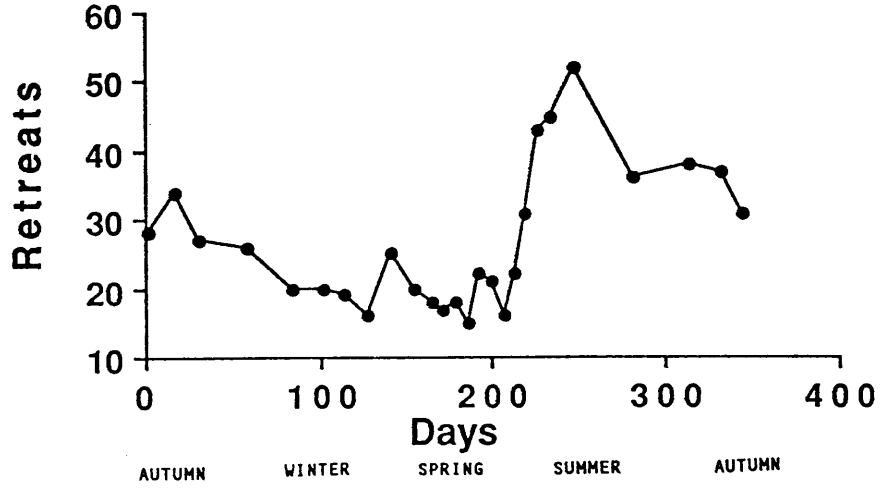

Figure 6.38 Total number of retreats counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

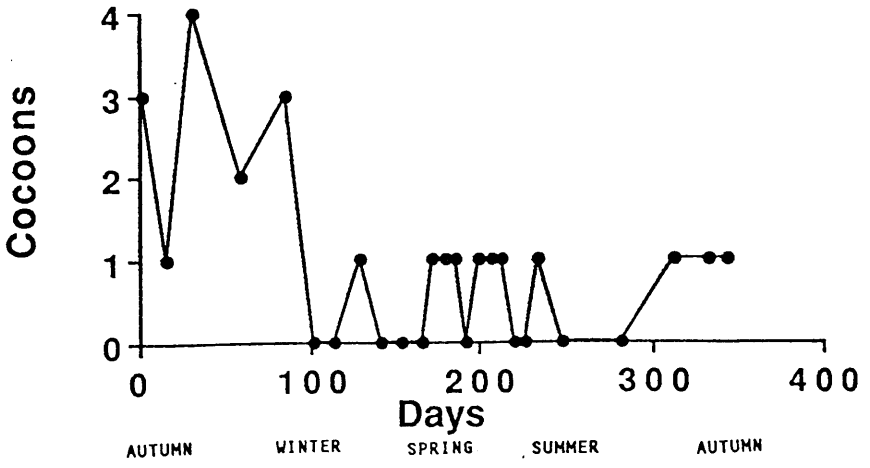

Figure 6.39 Total number of cocoons counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

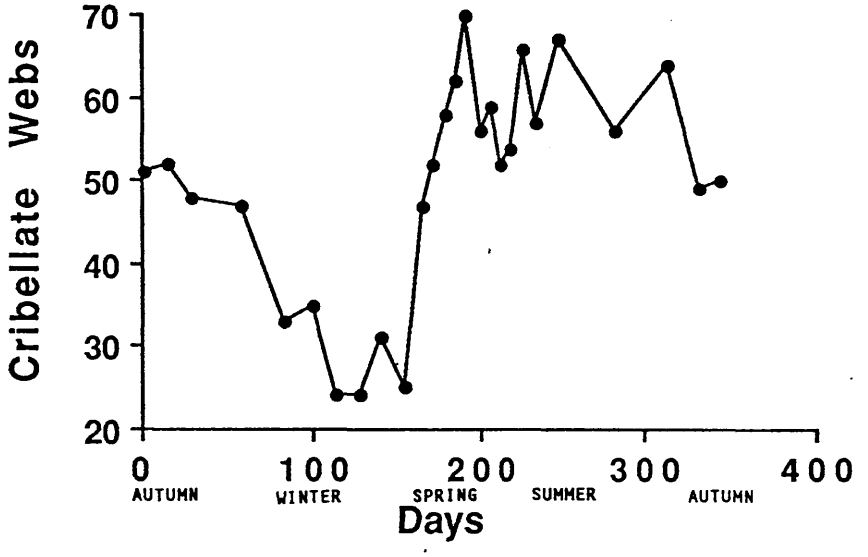

Figure 6.40 Total number of cribellate webs counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

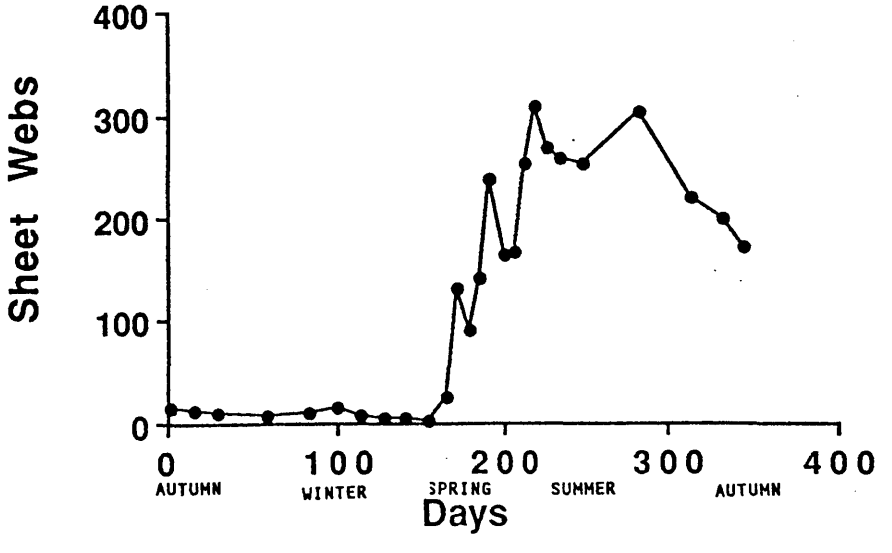

Figure 6.41 Total number of sheet webs counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

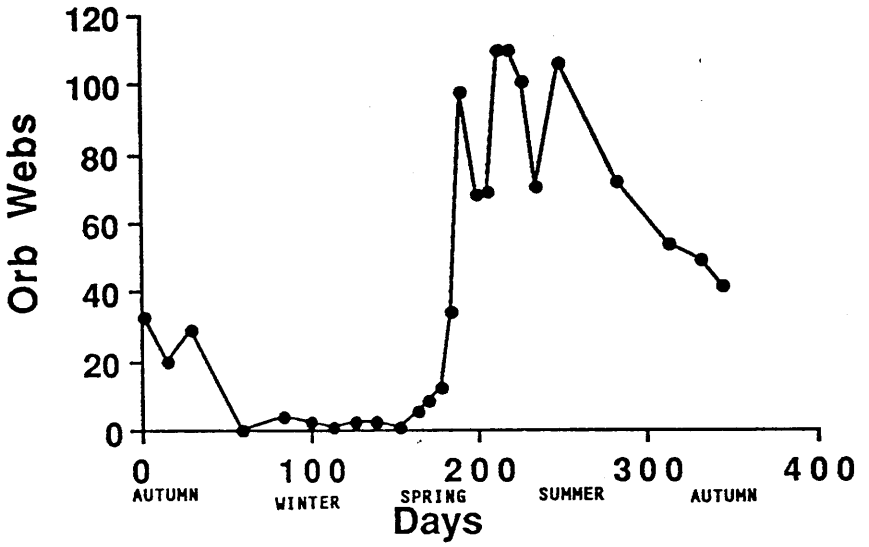

Figure 6.42 Total number of orb webs counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

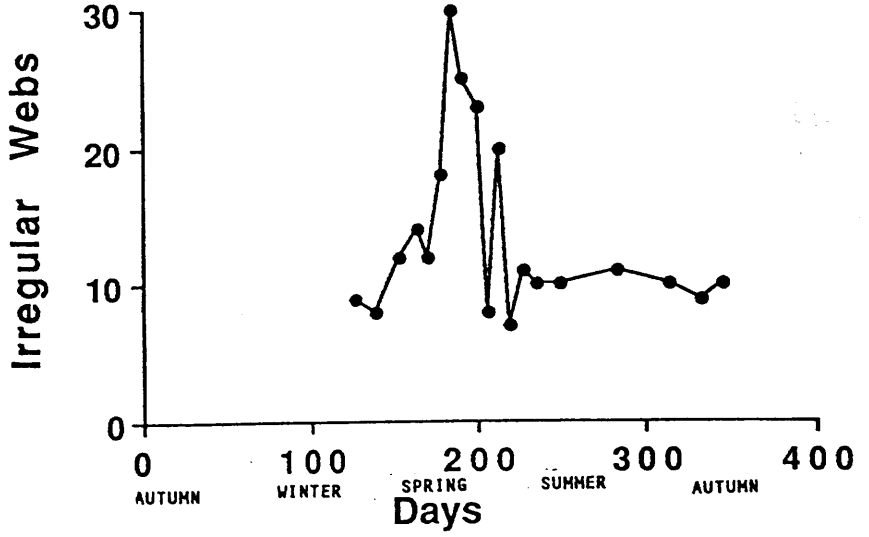

Figure 6.43 Total number of irregular webs counted in the study area through the year November 1989 - November 1990, combining numbers from all sites A-H.

shows a peak in total web numbers in late May (433 webs on Day 192 (24th May 1990)), and another in early summer (496 webs on Day 220 (21st June 1990)). There is also a less clear peak in August (448 on Day 282 (22nd August 1990)). From late summer, numbers decline more or less steadily through autumn and winter, and reach their lowest values in the first weeks of spring (46 webs on Day 128 (21st March 1990) and Day 141 (3rd April 1990)).

The number of orb webs (figure 6.42) started to recover from the winter low (just one or two found on each occasion between Days 101 and 154 (22nd February to 16th April)) at the end of April (around Day 165). At the same time, the number of ecribellate sheet webs (figure 6.41) started to increase, as did the number of cribellate sheets (figure 6.40). Irregular webs (figure 6.43) started to recover from winter rather earlier, in March (around Day 128). The irregular webs also reached their first peak one week earlier than the other types of web, which were all at a maximum on Day 192 (24th May). The late spring/early summer peaks for all four groups occurred within a fortnight of each other (Day 213 to Day 227, *i.e.* 14th June to 28th June), with the ecribellate webs peaking last. The mid-summer peak was less clearly defined, lasting from Day 248 (19th July) (106 orbs and 67 cribellate sheet webs) until Day 282 (22nd August) (304 sheet webs), and not showing at all in irregular webs.

The first fresh webs of the 1990 season were seen on Day 101 (22nd February). A few ecribellate and cribellate sheets had the appearance of being newly spun. The orb webs found during the winter months may have been intact spinnings from earlier weeks, or fresher spinnings of *Zygiella x-notata*, the only Araneid known to be capable of spinning during winter.

Figure 6.38, giving the number of retreats, has peaks coinciding with the first and third web peaks (22 on 24th May and 52 on 19th July respectively) and shows fewest numbers in late winter (16 on 21st March (Day 128)). Cocoons were not very easily found at the sites

examined and numbers recorded are much lower than for webs or retreats, but figure 6.39 shows more found in autumn and early winter (Days 1 to 84 (5th February)) than at other times during the year.

6.4.2.2) Site-by-site breakdown

The individual sites used were very different in their suitability for each type of spider-spinning. They ranged from man-made frames to a brick wall with and eaves, and from a dense bush to three types of tree bark. The types of silken structures found differed between the sites, as did the patterns of fluctuations, even within one family. Hence it is useful to examine the sites separately, to look for differences between them in the web-types (and hence families of spider) present and in the time of year each web, retreat or cocoon, is at its most abundant. Chaffinches could concentrate their search for silk in those sites that contain the greatest numbers of the most suitable types of silken structure.

A) Holly Hedge.

The dominant web-types were orb and sheet webs, with irregular webs occasionally seen. Numbers of both types were highest in spring and summer, with a decline early June (c. Day 200) and mid-July (c. Day 250). Autumn saw a decline in both and none were present in winter.

Retreats and cocoons were never seen on the holly hedge.

It was noticed that on 18th May the holly hedge showed the first signs of new growth as new shoots appeared.

B) Sign Post.

Orb webs were the dominant type, being present occupying all the available corners in the summer and autumn. One or two irregular webs were present during spring and early summer.

The number of retreats corresponded with the number of orb webs, and cocoons were never seen.

C) Carport.

Again orb webs were the dominant type in the frame work of this structure, appearing first in the middle of spring, though very small. These persisted into the summer, becoming larger and then declining from August into autumn 1990. Cribellate webs, belonging to *Amaurobius* sp, were present in the second half of the spring and summer, but were rare during the rest of the year.

The number of visible retreats again corresponded with the number of orb webs. One cocoon was seen once during spring (on Day 179, 11th May), and another during autumn 1990.

D) Bicycle Shed.

The outside wall of the bicycle shed provided suitable sites for all four types of web, but sheet webs were rare. Orb webs were commonest during June 1990 (Day 199 to 228) and irregular webs during May (Days 168 to 198). Cribellate webs were found throughout spring, summer and autumn, numbers being highest towards the end of May.

The number of retreats began to rise in late spring until mid-summer, being rare in autumn and winter. Cocoons were only present during autumn 1989, and then only numbering 4.

E - H) Trees.

The webs on the lower 6 feet of the two gean (wild cherry) trees (*Prunus avium*) and the beech (*Fagus sylvatica*) tree were mostly sheet webs, located in the buttresses. Only unidentifiable cobwebs, probably deserted sheet webs were present in autumn 1989 on the

two geans. Sheet webs were present in greatest numbers in spring and summer on these three trees, numbers starting to increase from the end of April (c. day 165). The details of the timing of the fluctuations differed between trees, implying that one tree can not be taken to be representative of the whole environment.

A few cribellate webs were present on these trees. The yew tree (*Taxus baccata*), on the other hand, provided an ideal bark for *Amaurobius* to lay its web over and to hide under. Hence cribellate webs were the dominant web-type on this tree. They were never uncommon during the whole survey period, but were found in greatest abundance between late April and October 1990 (Days 168 to 344).

Retreats and cocoons were never visible on the tree trunks.

6.4.2.3 Effect of time of day

The silk count was not carried out at a set time each day. Spider activity varies during the day, so the number of webs counted my differ between morning and afternoon. As described in section 5.5.1.1, to assess the extent of the effect of time of day upon the results, on four occasions, counts were carried out in both the morning and afternoon. The results are presented in table 6.8. This shows that the differences between morning and afternoon counts were generally very small. (Wilcoxon Test; $T = 81.5$, $N = 18$, $p > 0.1$).

One difference is large enough to alter the picture given above, that is the lower number of sheet webs counted on the afternoon of 22nd August. If the afternoon value is used, the August peak in sheet web numbers, and in overall web numbers, shown in figures 6.41 and 6.37 respectively, is removed. It also weakens the justification for the high number of sheet webs on 21st June. The apparent pattern of sheet web numbers would appear to consist of a fairly steady value from mid-June until late-August. However, no firm decision can be made about which picture is closest to the truth. Possible reasons for such variation are discussed in section 5.5.1.1, but it should be noted here that the light

Table 6.8 Comparison of morning and afternoon counts on four days of webs at all the sites at Garscube.

date	time of day	WEB TYPE Cob	Orb	Sheet	Cribellate	Irregular
28th June	11 am	13	101	268	66	11
	5 pm	15	103	269	62	12
6th July	11 am	9	71	259	57	10
	5 pm	11	82	260	58	14
19th July	11 am	9	106	252	67	10
	5 pm	7	101	268	65	10
22nd Aug	10 am	5	72	304	56	11
	4 pm	4	65	268	53	11

was noticeably poorer during the afternoon of August 22nd than the morning, decreasing the visibility of some sheet webs.

Other differences in morning and afternoon counts are too small to alter the picture described earlier, and so this time-consuming double count was abandoned.

6.4.3) Turnover of cocoons and retreats

The number of cocoons at the above sites are low throughout the year, so it was necessary to examine a further area where cocoons were more plentiful. The ceiling of the bicycle shed provided an ideal site. Furthermore, the longevity of individual cocoons and retreats could be determined by regularly mapping the position of the structures.

The cocoons found in each of the four sections amongst the rafters of the bicycle shed are shown in figures 6.44(A)-(D). Each figure shows a diagrammatic representation of the section, with the position of cocoons and retreats marked. For each structure, the date of the first inspection after their appearance, hatching and disappearance are given. Where no appearance date is given, the structure was present on the first date of inspection (10th January 1990), and likewise, where no date of hatching or disappearance is given, the structure was still in place and intact on 23rd August 1990. Figure 6.45 shows how the total number of cocoons changed during the observation period, again Day numbers representing the dates.

The number of cocoons on the ceiling inside of the bicycle shed was constant through winter at 21 from 10th January (Day 58) until 3rd April (Day 141). The total had declined by 2 by 3rd May (Day 171), and began to rise around mid-July (Day 248), reaching 24 by 23rd August (Day 283), when the observations ceased. Retreats began to appear earlier - around mid-May, and continued to be spun up to the end of the observation period.

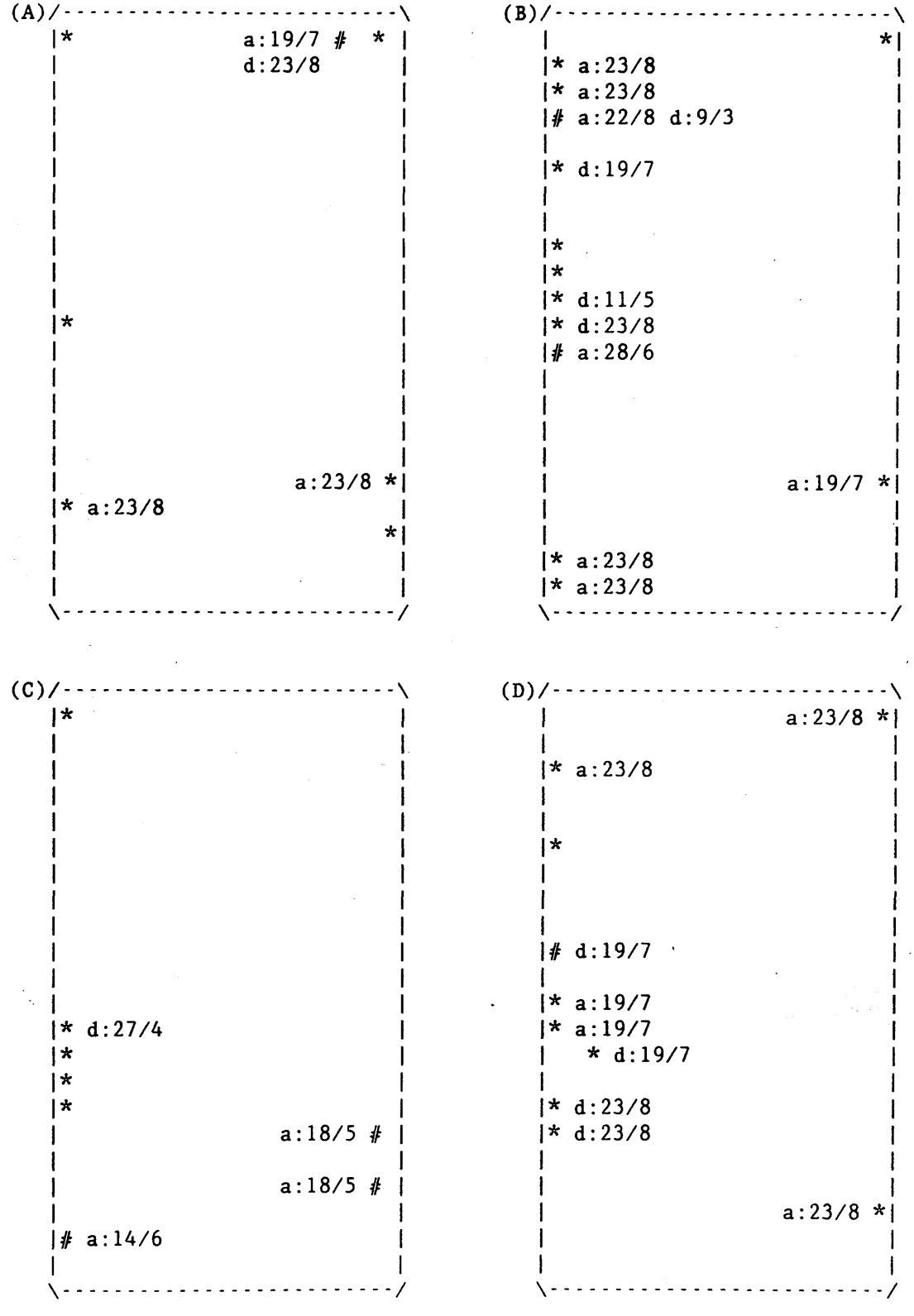

Figure 6.44. The positions of cocoons (*) and retreats (#) among the rafters of the bicycle shed ceiling at Garscube Estate (site D). Each of the four figures (A) - (D) is a separate section divided off by beams. The appearance (a:) and disappearance (d:) dates of the structures are given. Where no appearance date is given, the structure was present on the first observation day (10th January). Where no disappearance date is given the structure was present on the last observation day (23rd August).

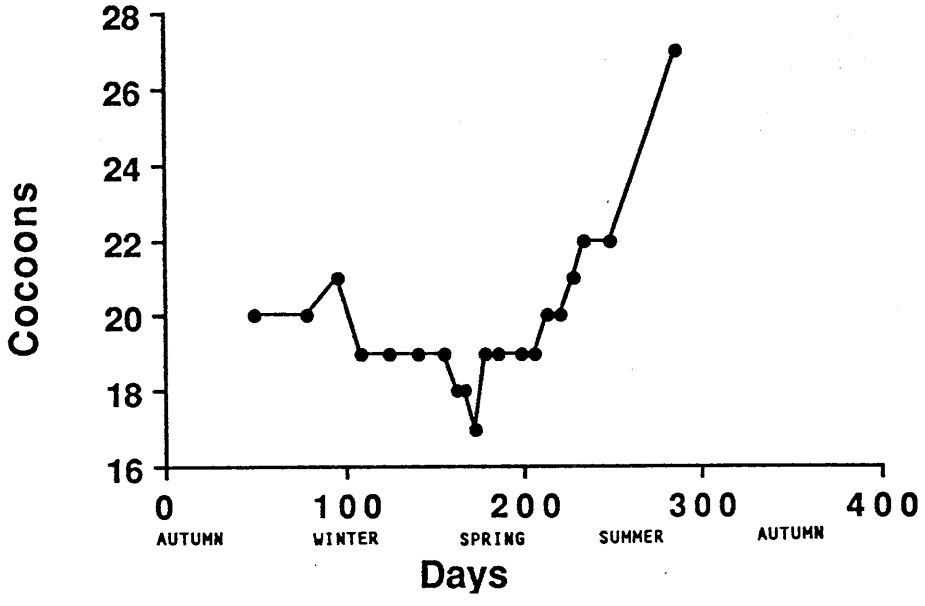

Figure 6.45 Number of cocoons in the four sections of the bicycle shed ceiling (shown in figure 6.44) during the period January - August 1990.

CHAPTER 7

CHAFFINCH NEST STRUCTURE AND THE USE OF SILK

The reasons for silk being used in birds nests, and the types of silk that are employed, will depend, in part, upon what other types of material are used in the nest, and how those materials are utilised. Hence it is necessary before looking at specific roles of silk, to examine the variation in composition of chaffinch nests. This allows the influence of other parameters of the nests on silk use to be examined.

7.1) THE NESTING MATERIALS EMPLOYED

The wide range of materials that were found in the nests examined may be a contributory factor to the chaffinch's success. Indeed, it may be the key to the birds' exploitation of such a wide range of habitats, in such a large geographical area (see section 2.3). Alternatively, it may be these properties of chaffinch populations that either allow or compel the birds to use a variety of different materials. Silk is just one of the materials that may be contributing to the chaffinch's success.

In the 38 nests I examined, enormous variation was found, both in the types of materials employed (a total of 21 - table 6.1) and the relative proportions of each type. However, relating the composition to habitat-type is very difficult, as demonstrated by just a few examples. The information upon which these comparisons are based is given in Appendix A.

Nests from the same habitat, but built by different birds, can show a strong similarity in structure and composition. For instance nests 29, 30 and 31, all from a pear orchard in Oxfordshire, are primarily made from moss and rootlets, with some grass and very little in the way of superficial camouflage. On the other hand, nests 36 and 38, found close together on scrubland in Devon, while showing a similarly narrow range of materials, have very different proportions of them.

Nests from similar habitats, in a similar region of the UK, can also show similarities. Two nests, one from mid-Wales, the other from north-Wales, both found in gardens on the edge of farmland, in wooded areas, (nests 28 and 32) have similar compositions. Both were moss-based, with grass reinforcing the structure. Wool formed a significant part. Layer A of both consisted of a wide range of materials, though the exact composition differed, and amounts of silk were similar (38 and 41 units respectively).

The various other nests found in habitats described as rural or country gardens fail to show any regular similarities. Nests 8 and 9, found in an ivy bush in a village garden in the Glasgow area, and probably built by the same female (section 6.2.2.1), show very little similarity.

There are examples, therefore, of nests from the same or similar habitats showing similar structures and compositions, but likewise, there are contrary cases too.

One element of this nest variation is the large range in the number of materials in individual nests. At the extremes, 2 nests have 11 materials, and 2 have only 5. This is worth investigation, as it may present solutions to explain the inconsistencies in chaffinch nest structure. There are two possible explanations for this variation:

(i) Individual nests with a large variety of materials were built by birds which did not have access to large quantities of the more suitable

materials, and had to make do with a variety of less appropriate ones. In contrast, nests with few different materials, were built in territories with an abundant supply of the most suitable materials. These birds would be able to ignore the other materials.

(ii) Nests with a large variety of materials have been built by exploiting a large range of materials specifically in order to confer advantages such as camouflage, strength or insulation. These nests originate from favourable territories. Nests with little variety were built by birds with access to only a narrow range of possible materials.

In order to distinguish between the two possibilities - good (i.e. successful) territories being the ones that produce nests with many different materials or nests with few different materials, data on the longevity and fledging success of nests would be useful. Unfortunately, no such data are available. A review of a wide range of nests from tropical regions of the world, has indicated that the number of materials in any one nest may be generally low, even in those nests with a complex structure (Hansell, pers. com.).

My data can be used to indicate which of the two alternatives may be the more likely in the majority of cases.

The versatility of chaffinches in their use of material can be seen in the nests described in Appendix A. For instance, bark, wood-chippings and paper appear to play a similar role to lichen in Layer A (the superficial layer) of the nests, that of camouflaging the structure, and blending it in with the vegetation. Silk may also occupy a camouflaging role in some cases, as will be discussed later. Lichen is evidently the most favoured of these materials for this role, being found so commonly in nests. It forms a surface of variable colour and texture. Indeed, lichen is used extensively by a very wide range of birds throughout the world to camouflage their nests (Speta 1986). This observation, that

Layer A can consist of a wide variety of materials, can be used to support either hypothesis. Either a better camouflage is produced when a wide variety of materials is used (therefore complex nests are favoured), or insufficient lichen is present in some environments, so necessitating the use of other, less appropriate materials. It is impossible to distinguish between these two without information about the success of different nest compositions, or about the complexity of the habitat. The latter may indicate how complex the camouflage should be, as well as how many different materials are available.

A second example of the birds' versatility is in the composition of Layer B. Although most nests are moss-based, a few chaffinches use other materials such as rootlets and cotton-wool to form the foundation of the nest. Long strips of bark or wood can also replace moss as the major structural material (see Appendix A). It appears that moss is normally the most favoured structural material, but a lack of availability may occasionally dictate its replacement by other materials. There is no apparent reason why these other materials, such as rootlets or bark strips, should not be available in most habitats. Thus, this observations provides better support for the hypothesis that simple nest composition, using few different materials, of high quality, are favoured.

Similarly, the majority of nests mix grass in with the moss to provide a fibrous reinforcement, but a few nests use animal hair in the same way, and contain little grass. The properties of both grass and hair would appear to be similar with respect to this reinforcing function, but the higher incidence of grass use would imply either that, for some reason, it is more practical, or that it is more available. Reasons for the greater suitability of grass may include the greater coarseness of grass stems, or their ease of manipulation. Nests with hair instead would be making do with what is available. Alternatively, hair may be in limited supply, and those nests that do include it in Layer B are those in more favourable habitats, able to exploit the properties of both grass and hair as reinforcing materials. One additional observation helps in distinguishing the two

possibilities in this case - the vast majority of nests included hair as a major component of the lining. This implies that hair availability is not generally low. Hence those birds that use it in Layer B do so due to a lack of suitable grasses. Therefore, the simple structure, using a small range of materials, is the preferred type.

Ideally, some form of diversity index of suitable materials in each territory would provide the information required about how much the chaffinches restrict themselves to a narrow range of materials. To help decide whether simple or complex structures are favoured it is useful to look at the nests that I found at Garscube, where the overall habitat structure is known, and the composition of each of the territories is also known, qualitatively.

If the study area were as good as the best mature deciduous woodland in supporting chaffinch breeding pairs, the area of 1200 ha (section 5.1) would contain around 20 territories (average size of 6,000m^2 from Newton 1972). Ten territories were identified. Less than half the area could be described as dense woodland. The rest is open woodland and parkland. Therefore, the observation of 10 territories within the area shows that Garscube provides a relatively plentiful habitat for chaffinches. We have already seen (section 5.1) that the Estate is very diverse in habitat structure, so we expect a wide range of materials to be available for use in the nests, and the materials will vary between territories.

Nest 2 was in a beech tree in a narrow strip of fairly open beech woodland, with small rhododendron and other bushes. Nest 3 was in rhododendron, and Nest 4 a yew tree in parkland-type habitat with a variety of trees and bushes, close to buildings. These latter nests were thus in a more mixed habitat, but contained fewer materials. We can not draw any firm conclusions from this observation, but it is interesting to note as evidence against hypothesis (ii) above. The materials present in each nest are given in Appendix A.

We should expect that two nests built in the same territory, or in neighbouring territories, to show similar compositions as a result of the same environmental pressures, restrictions and opportunities. Nests 3 and 4 (both 1990 breeding season) were probably built by the same female (section 6.2.2.1) and show similarities. Both had woody fibre playing a structural role, and lichen as the third most abundant material, with few pieces of bark. Nest 3 contained 7 materials and Nest 4 contained 8. Nests 1 (1988 season) and 2 (1990 season), both from Garscube, but built by different females, do not share these features, containing 10 and 9 materials respectively, and neither containing any woody fibre.

It must be remembered that none of these nests was successful. This could imply that the birds were not free to create the best structures, in spite of the variable habitat and the range of materials available. Reasons for failure appeared to include predation, disturbance and weak structure. This points toward the hypothesis that simple is best, using large amounts of a few materials, but the relatively small size of the territories at Garscube meant that insufficient supplies were available (Marler, 1956, and Newton, 1972, both suggest that nest materials are collected mostly from within the territory).

Time of nest-building is another factor involved in material availability, but only for Nests 2 and 4, from Garscube Estate, are approximate dates known, but some information is also known about Nest 3 (see section 6.2.2.2). Nest 2, in a young beech tree, was seen being built on 11th May. No lining was present, and Layer A was incomplete. The nest was therefore probably started around 6th May, assuming building lasts 7 days (Marler 1956). Nest 4 was discovered in a yew tree on 7th May, at or near completion, and so was probably started around 30th April. For Nest 3, the date of discovery (June 15th) suggests that it may have been built as a replacement for Nest 4, and so started after 7th May. Though destroyed by a predator, its state of completeness (there was a considerable amount of lining material around) indicates it was started

before 8th June. These proposed dates of construction are very approximate, owing to the considerable variation in nest-building duration (Marler 1956). Most of the nesting materials found in these three nests except for silk and dry grass - i.e. moss, lichen, rootlets, wool, twigs, paper and woody fibre - would be expected to be present all year round with little seasonal fluctuation. How time of construction can affect silk content will be discussed in the section 10.3.

Factors independent of habitat composition and time of breeding can affect the availability of certain materials. The presence of such materials as paper, string and other man-made litter will depend on the amount of human activity in the area, which is not necessarily related to habitat composition. The situation therefore is very complex and it is hardly surprising that, in a survey of 38 nests, patterns are difficult to spot.

It does appear that in most cases, the favoured nest composition is, like the general pattern world-wide suggested by Hansell (pers. com.), one that consists of a fairly narrow range of materials, and that those nests with the largest range are built in habitats containing insufficient quantities of the best materials. The requirements though, could be different in different habitats. Further, the ability of a chaffinch to assess what is required in any particular territory is unknown, and what rules of construction it may use to build the most successful nest have not been examined.

The implication of this conclusion for the variety of different chaffinch nest structures is that there are very few, ideal structures (perhaps only one) consisting of a moss and grass foundation layer, and a silk and lichen superficial layer. The large range of habitats that can be populated by the species means that the nest structure has to vary according to what materials are available.

This variety of nest structure, forced upon the birds by the habitat, can only be maintained if the birds are capable of employing different materials when they have to.

We have already seen the potential versatility of silk as a nesting material. This would allow silk to be used in a variety of ways, so making up for unsuitable materials, attaching or reinforcing them. We therefore expect to see the range of roles of silk in nests to be extensive, and dependent upon nest structure.

7.2) SILK AS A CHAFFINCH NESTING MATERIAL

Silk is the second most abundant nest material found in this study, in terms of the number of nests possessing it. Nest size varies over only a small range (section 6.2.1), and there is no evidence that larger nests require more or less silk than smaller nests, nor that simply by being larger, a nest can accommodate more silk (section 6.2.3.2).

Nest silk is concentrated in Layers A and B, with a small amount in Layer C and no silk at all in layer D (table 6.2). The deeper within the nest structure that the silk is found, the stronger the implication that it is used to hold the structure together from within. As there is little silk in Layer C, the major structural role of silk would be in maintaining the compactness and external neatness of the nest. The little silk found in Layer C may have been used to hold this layer together during construction, or placed there by mistake, if for example, too much silk had been collected. Alternatively, this silk could be playing a vital structural role in the few cases in which it occurs in this layer.

Reflecting the wide range of nest composition described in section 7.1, silk usage as a nesting material shows great variety. Silk is not an essential material, in that it is not present in every nest examined, as moss is. Silk is present in the vast majority (92%) of nests, though (table 6.1). Its wide range of special properties (section 3.4), and the wide range of silk types produced (section 3.2) mean that is can be used in several ways, even within one nest.

The three nests with no silk (Nests 25, 30 and 35) have several properties in common (see Appendix A) - twigs form a relatively large proportion of the materials present, and they have little in the way of decoration - lichen, bark, paper *etc.* are all absent or extremely insignificant. Two of them contain a large proportion of rootlets and the other has wood-strips playing a structural role. Very few other materials are present. It should be noted that these nests came from different habitats - one from a rural garden, one from a pear orchard and the other from open moorland. The nest characters described are not themselves unique to these nests, but the combination is.

This provides a good indication as to what roles silk may be playing in the other nests. Two roles are implied by the above - the attachment of pieces of other material in Layer A to the nest, and the improvement of the structure of Layer B.

The positive correlation between the amount of silk and the amount of lichen, coupled with the positive correlation of the amount of silk attached to lichen with the amount of lichen (table 6.4), shows that holding lichen, a material commonly found in layer A, is a widespread use of silk. Indeed, I noted that over 30% of silk units were attached to lichen, and the vast majority of lichen was attached by silk. This confirms the unsupported statement made in several nest identification guides (e.g. Witherby *et al.* 1938), that chaffinch nests are externally decorated with lichen, held on by spider silk. 1 silk unit on average binds 3 pieces of lichen to the nest.

Other materials commonly found in Layer A show a less clear relationship with silk. Around 15% of silk units found were attached to bark or wood, and there was a trend, though not significant, for nests with more bark or wood to have more silk units attached to the material (table 6.4). There is a problem here in that long strips of bark, which may have several silk units attached to each of them, are counted as the same as small wood chippings, several of which can be attached to one silk unit. Also, in some cases, these

long strips form a major part of Layer B and are woven into the nest, not requiring silk to hold them.

The same problem applies to twigs, which do not show any trend with numbers of silk units (table 6.4). Those twigs that form the base to which the nest is attached, and around which Layer B is constructed, do not form part of Layer A, but are still included in the analysis. Silk attached to these twigs forms the base adhesive. Voipio (1988) claimed that this silk is important in fixing the nest and making it firmer, and cases where such an adhesive is absent are anomalous. It is undoubtedly true, from examination of nests *in situ*, that tying the nest to surrounding twigs is a very common use of silk. Only 7% of silk units are attached to twigs (table 6.5), but 22 of the 30 (73%) nests that possessed both silk and twigs, had silk attached to the twigs. However, not all base twigs examined in this study had silk attached to them, implying that attaching the nest to its base is not such a universal function of silk.

Of the materials lichen, bark, wood and twigs, more silk is attached to twigs than to the others (see section 6.2.3.5). This implies that twigs, being larger, on the whole require more silk to hold them in place than the other, smaller, materials. Moreover, it is an additional indication that attaching twigs to the nest (or attaching the nest to twigs) is an important function of silk.

The other major use of silk apparent from the data, is in the roles 'embedded in' and 'stretched through' Layer B (table 6.5). These, particularly the latter, give the impression of a binding function of silk, holding the nest in its typically compact and neat form. Over 35% of all silk is used in this layer of the nest, and all but one of the nests that contained silk used at least one unit in this manner.

Silk units 'Embedded in Layer B' could be providing one of several functions: they could be binding the Layer together; they could themselves be acting as camouflage,

breaking up the monochrome of the green moss and grass; or they could have been intended to attach some other material, which either was never collected by the bird, or later fell off. Which of these possibilities applies to the units is unclear. If the type of silk 'Embedded in Layer B' is different from the type used to attach materials in Layer A, we could rule out the last possibility. Silk types are discussed in chapter 8.

Whether silk is used whenever available, or only when the other materials used necessitate it remains unclear. Marler's (1956) assertion that silk collection is extremely time-consuming would imply that those birds that do not use silk will gain an advantage in having to devote less time and energy to nest-building. Since nest-building uses up to one-third of daily metabolism (Dolnik 1982), and an average of over 8 hours per day for more than 5 days (Ilynia 1982) (section 2.5), any reduction of costs by using less silk would be advantageous. How the future success of the nest depends upon silk content is unknown. It could well be the situation that the nests collected for this project nearly all contained silk because they are more persistent than nests without silk. If having no silk means having no camouflaging Layer A, nests will only be successful in circumstances where predator numbers are low, or if the habitat requires less specific camouflage in order for the nest to blend in.

In order to emphasise the importance of silk, we can compare its use with that of wool. Silk and wool have some closely similar properties. Elasticity of wool ranges between 30% and 70%, depending upon the humidity under which the tests were carried out, and the rate of extension. This compares with typical figures for web frame silk of 25-40%, and for cocoon silk of 50-100% extensibilities. In wool, as in silk, the higher the humidity and the slower the rate of extension, the greater the extension that can be achieved (Alexander *et al.*, 1963). Wool fibre diameter is typically around 40μ (Astbury and Street, 1931), about 10 times coarser than orb web silk fibres, and 5 times coarser than cocoon fibres. Wool tensile strength has been calculated as 0.22 - 0.34 GNm^{-2} (using data from Astbury and Street, 1931). Values given for web frame silk are higher,

typically 0.8 - 1.7 GNm^{-2}, but cocoon silk, whose tensile strength is around 0.35 - 0.5 GNm^{-2}, is only slightly stronger than wool fibres. The greater coarseness of wool fibres makes them stronger.

Furthermore, the amino-acid composition is similar to many silks, the primary constituents being arginine, glutamic acid, cysteine, leucine and serine (Alexander *et al.*, 1963). However, Harris *et al.* (1942) give data showing the breaking strength of silk (type not given) being three times higher than that for wool, and attribute this to a higher amount of the short-chain amino-acids glycine and alanine.

An additional property of wool is its directional friction - movement from tip to root meets with greater resistance than from root to tip, owing to the surface properties of the wool fibre (Alexander *et al.*, 1963). This could be exploited in using wool to attach other materials, or to hold Layer B more firmly together.

To summarise, the differences in physical properties between wool fibre and cocoon silk fibre appear to be small - wool has slightly lower tensile strength, though it is coarser, and elasticity is similar for the two types of fibre. Even if these properties are not similar enough, if one function of silk is camouflage, wool might be expected to be able to substitute for silk. Wool may in fact have advantages over silk, in that it is stronger because of its greater coarseness, and the one-way added friction may make it more suitable.

However, data collected for this project show that the circumstances in which wool appears are not parallel with those for cocoon silk (see section 6.2.3.4). Wool is not used as a silk substitute, except on rare occasions - I noticed wool sometimes holding on lichen in those nests where silk content is low. Also, Tomek and Waligora (1976) say that the nest can be fastened to its base with woollen shreds in place of the silk which is so essential according to Voipio (1987).

In my study, there is not a positive correlation between amounts of the two materials, which would show that where demand for one is high, demand for both is high. Nor is there a negative correlation, which would indicate that one could take the place of the other (see section 6.2.3.4). Reinforcing the view that cocoons and wool are put to different uses, are the data giving web:cocoon ratios. Where the ratio is high, indicating that there are significant amounts of silk in the nest but cocoons are scarce, wool is no better represented (section 6.2.3.9). Thus wool does not make up for a lack of cocoons.

Part of the reason for this last observation could lie in the revelation that web and cocoon silk are put to slightly different purposes, although the role of one considerably overlaps the role of the other. The percentage of cocoon units in a nest that are 'embedded in' or 'stretched through' Layer B is significantly higher than the percentage of web units, though both types are involved (section 6.2.3.8). There is also a significant correlation between cocoon units and pieces of lichen but not between web units and pieces of lichen (section 6.2.3.7). It therefore appears that cocoon silk is used in these specific roles, whereas web silk is used as a more general nesting material, perhaps more versatile. The larger sample size involved with cocoons, and the higher number of these units, may make these correlations easier to prove statistically. It can be readily imagined that the rough surface of moss and lichen can be entangled by the coarser and less flexible coils of cocoon silk more easily and strongly than by those of web silk. Web silk, on the other hand,is more easily malleable and so can be stretched and pulled more easily to fulfil a larger range of binding functions, such as tying the nest to twigs, and attaching the smoother additional materials.

It is not known whether different types of cocoon, from different species or families of spider, are used in a different range of the roles described above (see section 8.2 for an account of the types of cocoon that were found in the chaffinch nests).

The number of cocoon units was more than twice the number of web units in Layers A and B, and in Layer C (see table 6.4). Retreat silk was so rarely distinguished that no tests could be performed to investigate how it is used. The possible reasons for there being more cocoons used than webs are three-fold: (i) that suitable cocoons are more easily available in the environment, in terms of abundance and/or accessibility, (ii) that they are more suitable as a nesting material, or (iii) that both are suitable, but for rather different purposes, and the purposes to which cocoon silk is put occur more frequently. As we have already seen, the use of cocoon silk appears to be rather more specific, with web silk taking a more generalised role in the nests. This reflects the assertion that web silk may be more versatile, possessing properties of strength and adhesion that cocoon silk does not match, while on the other hand, cocoon silk, being coarser, more regular and appearing in larger bundles, may be more appropriate for the specific roles of attaching lichen and holding moss together.

The role of providing camouflage, which appears in the data included under 'embedded in' Layer B, and possibly 'stretched through' Layer B, could be attributed to both silk types equally, with cocoon silk having the possible advantage of presenting a wider choice of colours. However, in Garscube, the only colours available during nest-building were shades of yellow and golden brown for cocoons, as well as the white or greys that they have in common with webs. Some cocoons with a blue hue were seen later in the year at Garscube, but no other colours of silk were found in any nests from anywhere in the UK, so it is reasonable to assume that either these are the only colours available, or the only colours suitable, bearing in mind that the nest structure is usually green due to the moss. This contrasts with the accounts of green cocoons in Australasian bird nests (North 1904) (see chapter 1), even in those that are based upon a moss structure.

It now seems clear that one of the important factors in the success of the chaffinch in breeding in a large range of habitats in a large geographical area is its ability to use silk in

its nests. This allows a far greater range of materials to be used in the nests, decreasing the importance of searching for only the most favourable ones.

CHAPTER 8

IDENTIFICATION OF SILK UNITS FROM CHAFFINCH NESTS

8.1) TYPES OF SILK FOUND

8.1.1) Types of web silk found

All web silk collected from the 6 chaffinch nests that were involved in this part of the study - Nests 1-4 from Garscube Estate, Nest 29 from the pear orchard in Oxfordshire, and Nest 33 from Argyle (which contained no web units) - contained silk resembling closely the cribellar fibres visible in the web silk of *Amaurobius* (e.g. compare the micrographs in figure 6.27, web silk from Nest 1, and figure 6.4, amaurobiid web silk). Cribellar puffs are identifiable still intact in some cases (e.g. figure 6.28 from Nest 29, and figure 6.30 from Nest 1). In other cases, where the puffs have broken up, the cribellar silk can be found covering the coarser fibres. The two units of web silk examined from Nest 4 appeared to differ under the light microscope. These differences were primarily of colour, which can be variable according to age of the web, and how much dirt it contains. Hence it is still entirely possible that they are of the same species of spider.

No examples were found of web units taken from chaffinch nests that did not contain cribellar fibres. With regard to the nests from Garscube Estate, the only cribellate spider found was *Amaurobius*, so it is very likely that the silk was spun by this species. I can not be this certain about the silk in Nest 29 from Oxfordshire, since silk from other amaurobiids or members of other cribellate families may have been available.

8.1.2) Types of cocoon silk found

Identification of cocoon silk proves more difficult. We have seen in section 6.3.1.3 that within a single species, the silk from cocoons can be very variable. There is overlap of some features between species from different families. Cocoons from only three species of spider were examined - *Amaurobius fenestralis*, *Steatoda bipunctata*, and *Zygiella x-notata* (see section 6.3.1.3). We can not therefore expect that much cocoon silk removed from nests will show strong similarities with any of the known silk.

A few cases, such as Sample I from Nest 1, in micrographs 31-32, pose little problem. It resembles closely *Zygiella* cocoon silk (see figures 6.14-6.18) in fibre diameter (coarse = 4μ, fine = 2μ), in the predominance of the coarser fibre, and in the surface detail of the coarse fibres, as well as in the colour of the cocoon. However, Sample A, which again resembles *Zygiella* cocoons for the same reasons, contains some silk that looks like cribellar (See the low power micrograph in figure 6.33). This may have come from web silk placed adjacent to the cocoon in the nest, or have remained attached to the bird's beak between trips to collect silk. Or else the cocoon may really have been spun by a cribellate spider. This latter seems unlikely since the cocoon does not resemble the cocoon collected from the *Amaurobius* shelter (figures 6.22 - 6.25), and no other cribellate was discovered at Garscube.

Other cocoon silk examined resembles the *Zygiella* silk, but without such distinct ridging on the coarse fibres. These cocoons may have been spun by close relatives of *Zygiella*, such as other araneids. The apparent resemblance of Sample O from Nest 1 to *Zygiella* cocoon silk is based on the large proportion of coarse (5μ) silk, little finer silk, and no double or multi-stranded threads. Unfortunately, we do not know whether the irregular ridging is restricted to *Zygiella x-notata*, to the genus, to related genera, to the whole family, or if it is even more widely distributed than that. Sample U of Nest 1 has silk with

similar ridging, but none of the other properties of *Zygiella* silk described in section 6.3.1.3. Rather, it contains a large range of fibre diameters, and double- and multi-stranded threads. Parts of the sample are more reminiscent of amaurobiid cocoons, with areas of anastomosis. The sample was a brown/grey colour.

It is not surprising, bearing in mind the range of spider species whose cocoons are available to birds at Garscube (table 6.7 lists those species found, but is not intended to include all species present), that most cocoon samples from Nests 1-4 do not show any similarities with those of the three known species (e.g. Sample V, Nest 1, figures 6.34 - 6.36). None of the cocoon silk from Nests 2 and 3 resembles them, though the predominance of coarse (4μ) silk and single-strandedness of both cocoon samples from Nest 2 and two of the three from Nest 3 may mean they are araneid or similar silk. The colour of these is again a yellow or golden brown. The third sample from Nest 3 is also similar, but the coarse silk is slightly finer (Around 3μ), and there are some double-stranded threads.

Two samples from Nest 4 could have been spun by araneids for the same reason, but the other two Samples are very different, being composed of large bundles of silk, some bundles being of coarse fibres, others fine.

Nest 33, from Argyle (where the spider population has not been looked at), contains cocoons consisting of single-stranded fibres of uniform diameter (around 2μ), and so may also belong to an araneid, although the silk was white. In this nest, all the cocoons were identical in appearance under the light microscope.

Table 8.1 summarises these suggestions for the types of cocoon present in the five nests examined.

Table 8.1. Number of different cocoons in 5 nests examined. No two cocoons from the same nest appeared the same, apart from *Zygiella* cocoons. All identifications are tentative.

Nest	Total number of cocoons examined	Number of *Zygiella*	Number of other Araneidae	Number of non-Araneidae
1	7	2	1	4
2	2	0	2	0
3	3	0	3	0
4	4	0	2	2
33	1	0	1	0

8.2) PROBLEMS WITH THE METHOD OF IDENTIFICATION

Identifying silk by microscopy has proven difficult. Silk, especially web silk, attaches dirt as easily as it attaches insects. In their attempts to escape from webs, insect shed scales and hairs, which remain attached to the silk (Eisner *et al.* 1964). These are very difficult to remove completely before the web is examined, and will confuse the appearance of the silk at both high and low power.

Even if obtaining clean samples of silk was possible, how similar the silk of different members of the same family can be, is unclear. Only fourteen species of spider were collected, and the silk of only ten of these examined (table 6.5(a)). Even within one species, as we have seen with *Zygiella x-notata*, there is considerable variation in the appearance of the silk threads under electron microscopy.

In some cases, I have tentatively suggested that one unknown silk unit is similar to the silk from a spider collected at Garscube, and thus may have been spun by a related species. Which, if any, features of silk should be considered important in such comparisons is not known. This, added to the doubts about phylogeny, means that in order to be at all certain about the identification of silk, a far larger range of species ought to be examined. It was fortunate from this point of view that all web silk contained cribellar fibres, and that only one species of cribellate spider was found at Garscube.

Cocoons were less well studied than webs. The reasons why cocoons of only three different species of spider were collected are two-fold. Firstly, the successful passing on of genes to the next generation depends in most species upon the survival the contents of one single egg-sac, which usually is not protected by the mother. Hence the cocoon is spun in the most inaccessible places, so that it is not damaged or destroyed by predators or the elements. Hence the structures are very hard to find. Secondly, for a cocoon to be of any use in this study, the female that spun it must be close by when it is found, in order that the

species the cocoon belongs to can be ascertained. Again in most species the female deserts the cocoon after it has been spun, so there is only a very short period of time when the cocoon is at or near completion and the female is still nearby. *Zygiella* cocoons were the most frequently found, and it is the female of this species that can remain active during the winter, after egg-laying (see Appendix B). Hence, the female remains near to the cocoon for a longer period of time.

The chaffinches are not faced by the same restrictions as the collector, being able to search in less accessible places, and not having to find the spinner nearby. Indeed, chaffinches appear to find cocoons far more plentiful in the environment of Garscube Estate than I did. Cocoon silk in the nests was generally more common than web silk in the same nests (see Nests 1-4 in appendix A), but very little cocoon silk was found during the survey at Garscube (figure 6.39). This implies that the range of cocoons available is larger than the three species described in section 6.3.1.3, and so identification of the cocoon silk with any certainty is impossible using the data gathered in this study.

To summarise the findings here, all web silk found in the 6 chaffinch nests examined is from cribellate spiders. For the 4 nests from Garscube, this study shows the genus concerned probably to be *Amaurobius*.

The cocoon silk posed more problems in identification. A few units were similar in appearance under light and scanning-electron microscopes to cocoon silk spun by *Zygiella x-notata*, and so may be from either this species or a related one. However, it is not known which are the features of the silk that are best conserved between related species, making such suggestions at best tentative. Other cocoon units from the 6 nests bear little resemblance to any of the cocoons from identified species examined in this study. The small number of species whose cocoon silk was examined means identifications can not be made with any confidence.

CHAPTER 9

FACTORS AFFECTING CHOICE OF SILK BY CHAFFINCHES

9.1) ABUNDANCE OF SILK THROUGH THE YEAR

A picture of the relative amounts of spider silk present in the environment throughout the year can be created using information from the study of web, retreat and cocoon numbers at the sites at Garscube Estate, coupled with predictions from accounts of the life histories of the 14 spiders found at Garscube, as given in Appendix B.

9.1.1) Web silk changes through the year

Using the information described above, I here consider how the number and extent of webs of each type changes during the year.

9.1.1.1) Orb Webs

The orb-spinning species found at Garscube were *Meta segmentata*, *Araneus diadematus*, and *Zygiella x-notata*. All three become mature in the autumn (though *A. diadematus* takes two years), and overwinter as eggs which hatch in the spring. Therefore, during spring, the number of webs found will rise as the eggs hatch. At this time juveniles predominate. As the year progresses, the spiderlings moult and grow, while the population declines (see Appendix B). We therefore expect to see a late spring peak in the number of orb webs (although these are mostly small, being spun by juveniles), followed by a steady decline in number but increase in their size. By winter, virtually no orb webs will be present (*A. diadematus* sub-adults are in torpor, but *Z. x-notata* females can remain

active). The predicted decrease in numbers is borne out in figure 6.42. As the year progresses the population declines through mortality, although the survivors grow and produce larger orbs.

It has been demonstrated (Leborgne and Pasquet 1987), that web size in the other common araneid, *Zygiella x-notata*, is reduced in high population densities, and that there is a tendency for conspecifics to congregate. This will tend to reduce the size of individual webs, but increase the amount of silk in any one area. How this may affect chaffinches in their search for nesting material is unknown. Orb web silk has not been found in the nests examined, although it is possible that some may be present, but in quantities too small to be seen during my examination. In either case, the effect of the spiders congregating will be minimal. If large tropical araneids show similar behavioural responses, birds could take advantage of the resulting high density of sticky silk. This point will be discussed in section 11.5.

9.1.1.2) Sheet Webs

The sheet web spiders (Linyphiidae) found at Garscube vary in their life histories. *Bathyphantes* spp and *Lepthyphantes* spp can be found as adults all year round, but *Stemonyphantes lineatus* is mature in autumn and winter. The other three species found reach maturity in early summer (see Appendix B). Therefore, small webs spun by juveniles and larger webs spun by adults can be found at any time during the year. The relative proportions of large and small sheet webs will depend upon the relative abundances of the species concerned, and change through the year. Information on relative numbers of spiders was not collected, though I noticed that a large proportion of sheet webs found early in the spring appeared to be spun by *Stemonyphantes lineatus* juveniles, and were consequently very small. Sheet webs are more persistent than orb webs, so a significant proportion of those found could be disused, the spider having died or spun a new web nearby. It is, therefore, not easy to predict from the life history of this family, how sheet web numbers might vary through the year, but the picture produced in

this study of their abundance is very clear. Their is a high number of webs following the rapid rise in spring, which remains reasonably constant through the summer. From autumn there is a steady decline in numbers until the winter low.

9.1.1.3) Irregular Webs

The three species of *Theridion* found in this study mature in the early summer, with the adults often remaining active into winter. They are juveniles in autumn, which over-winter as sub-adults (see Appendix B). Hence we might expect the largest number of irregular webs to be found in the autumn, before the winter kills off many juveniles. The remaining spider, *Steatoda bipunctata*, matures in the autumn, and the female can live for up to 4 years (Appendix B). A spring peak in numbers would result from this. In this study, numbers were highest in the middle of May, implying the influence of *Steatoda*, and perhaps other species that were not found but are juvenile at the same time, build the majority of irregular webs. It should be noted that irregular webs were only looked for from the middle of winter 1990 onwards, finishing in autumn 1990.

9.1.1.4) Cribellate Webs

In this study of spiders found at Garscube through the year, juvenile Amaurobiids were no smaller than adult Araneids, and so generally spun webs as large. Furthermore, the web is continually added to, rather than replaced every day or so (see section 3.5). Consequently, after a few days it can be quite extensive. Ecribellate sheet webs are replaced occasionally, but once constructed are not enlarged. *Amaurobius fenestralis*, the only cribellate spider found at Garscube, can be found as adults or sub-adults during the whole year, since the female over-winters between mating and oviposition and the juveniles take up to eighteen months to mature. So during the chaffinch breeding season, juveniles larger than the adults of the other families, and adults, are spinning and adding to large cribellate webs. Webs were found at Garscube all year round, with the greatest number present in late May, though these were not all as large as those found later in the year.

9.1.2) Cocoon and retreat number changes through the year

Cocoons are spun by a far greater range of spiders than just the fourteen web-spinners I collected (table 6.7). Therefore, accurate predictions about the abundance of cocoons through the year cannot be made. All that can be said is that in general, across all families, most cocoons are constructed in autumn, in those species that overwinter as eggs, or spring, in those species that overwinter as sub-adults or adults. My cocoon count inside the bicycle shed (figure 6.45) clearly shows that the highest number of cocoons was in summer 1990, as was the greatest number of fresh cocoon spinnings. The day on which the greatest number of cocoons appeared at this locality was on 23rd August (Day 283) when 9 appeared. The next highest was 3 cocoons appearing on 19th July (Day 248). The time of fastest disappearance was again on 23rd August, when 4 disappeared, and on 19th July when 3 disappeared. The reasons for the disappearances are unknown, but probably not due to hatching, as there were no remains. There was, therefore, a comparatively high turnover of cocoons during the month up to 23rd August, and during the fortnight up to 19th July.

The number of retreats counted on each occasion do not give an indication of the number of spiders present for several reasons. Firstly, not all species or families build retreats. Adult males that do not spin webs spend all their time searching for a mate and so do not need a permanent base. Retreats are designed to be extremely resilient, both to the elements and to attacks by potential predators. This means they can persist until well after the owner has died or built a new retreat. Finally, retreats were only visible on the bicycle shed, the carport and the sign-post, since those built in vegetation are concealed under bark or leaves. Most retreats counted were spun by Araneids, this being the dominant family in these man-made environments.

It is therefore the case that the amount of retreat silk present and visible in the

environment is not predictable from spider life histories. The data obtained show little pattern in the fluctuation in numbers, though there is a noticeable peak during late June and July. This is echoed in the new retreats being found on the ceiling of the bicycle shed around this time. The lowest point occurred in May. As for cocoons, this could be a reflection of the silk being collected by birds for their nests during this period, though it was never seen to occur, and little retreat silk was identified with any certainty in the chaffinch nests examined.

9.1.3) Comparability of successive web counts

The time of day when silk collection takes place in the chaffinch, or even whether they are restricted to a certain part of the day at all, is not known. Therefore, counts had to be made at all times of day. Some variation in numbers counted in morning and afternoon is inevitable, and can be attributed to various reasons: (1) different light conditions, affecting visibility of particularly the finer aerial webs; (2) real differences in the number of webs as some are spun and others destroyed during the day; (3) weather conditions immediately prior to the count - windy or wet weather can destroy webs and cold will discourage activity; (4) the difficulty in distinguishing between certain web types - especially irregular webs and smaller cribellate webs from a distance, and sheet webs and those irregular webs that include a rudimentary sheet; (5) the unreliability of the number of cobwebs, since when a single web is broken but not destroyed, it can be counted as two or more cobwebs.

In order to test how comparable the web counts are with one another is demonstrated on the four occasions where two counts were made on the same day. When two counts were made on the same day, little difference occurred between them (table 6.8, described in section 6.4.2.3). Even when light conditions were vastly different between them, on 22nd August, the difference in web numbers was not more than 15%.

Hence the numbers for each count are only as accurate as the complications listed

above allow, depending especially upon light and weather conditions. It is evident that, with a margin of error of up to 15%, some of the apparent fluctuations in figures 6.40 - 6.43 may not be real. Even so, the general trends are clear, due to the large changes in web numbers through the year.

9.1.4) Limitations of data in representing the whole environment

The sites selected for the silk availability survey represent a cross- section of the habitats at Garscube Estate. However, within any particular chaffinch territory, the combination of man-made and natural sites for spider spinnings is unlikely to be the same. Indeed, several of the observed territories contained no similar man-made structures where retreats or cocoons are poorly concealed.

Furthermore, there are differences between the sites chosen in the pattern of fluctuation of web numbers. Even a comparison between the three deciduous trees, all dominated by sheet webs, showed differing times for increases and decreases in web numbers (see section 6.4.2.2). This can be attributed to any of three factors: (a) each tree contains a different range of sheet-spinning species, whose populations fluctuate differently; (b) each tree presents a different set of microhabitats, leading to different behaviours of the spiders present; and (c) the limitations of the method of counting webs as described earlier for the comparison of counts made on the same day. These possibilities may also apply to other web-types and other sites. We do not know what species are present at each site, so we can not determine which of these factors is the most important.

With regard to retreats, only the man-made structures revealed any. The spiders conceal their retreats very well in vegetation. It is possible that a bird hunting for nesting material would learn, through natural selection or experience, where to search for these structures - typically under leaves, bark and stones. However, without any firm indications

that chaffinches do use retreats in their nests, it was not considered worthwhile to search harder for retreats.

Cocoons were not well represented in my silk availability survey. It was necessary to look inside the bicycle shed to find them in any quantity. One would expect all adult females (approximately half the adult population) to spin cocoons, but far more adult females were found than cocoons. Therefore, the survey is not representative of the availability of cocoons relative to webs. Further, more cocoon silk than web silk was found in the nests (see section 6.2.3.6), and so the supply must be rather greater than this survey indicates, the birds searching in places not examined. How cocoon silk availability may affect where and when to breed is therefore not as easy to assess, but the same principles apply as shall be used for webs in the following sections.

However, birds can collect silk from a wide range of locations within their territory, and so the combination of data from all the sites studied does give a realistic picture of the availability of silk in relative, if not absolute, terms. Therefore, we can decide which sites may be most suitable for which types of silk, and during what part of the spring would be ideal to collect the silk, and so when to commence nest-building. These are considered in the next sections.

9.2) RELATIVE AVAILABILITY OF SILK TYPES DURING CHAFFINCH BREEDING SEASON

9.2.1) Web silk

We have seen that the abundances of the four web types - orb, sheet, irregular and cribellate - change relative to each other during the year (see section 6.4.2). The relative abundance of each while the chaffinches are nest-building may contribute to the choice of web. The relative size of these webs will also be important. A larger web may be both

more visible, and more useful in the roles described in section 7.2. Generally, a larger spider spins a larger web, made from coarser, hence stronger, silk (*e.g.* Craig 1987a, and see section 3.4.1).

The data in figure 6.37 (see section 6.4.2) show that spider activity was lowest during the winter (January to early April 1990 (Days 58 to 141)), although it never completely ceased, and highest in late May (Day 192) and during the summer (late June to August (Days 227 to 282)). The crucial period as far as the chaffinches are concerned is the spring months, when nest-building occurs (section 6.1). This can cover the period of mid-April to mid-May nationwide, and in birds that build more than once, on into June. The first-nest period coincides with the start of the rise in web numbers, as seen in figure 6.37.

During this period, the most common webs at my sites at Garscube were sheet, with cribellates as the second most common. This can be seen by comparing the mid-April (Day 153) to Mid-May (Day 183) periods in figures 6.40 - 6.43. Orb web numbers did not reach comparable levels until the end of May, and irregular webs were never very abundant. The sites were chosen to provide a good cross-section of the areas within Garscube Estate, with the aim of providing numbers of each web-type that are representative of the whole environment. The reliability of the figures obtained is unclear, and the types of site present within each chaffinch territory will differ, but the overall picture created provides the best basis upon which the relative abundances of silk-types can be assessed.

I found both orb and sheet webs at Garscube Estate to be small during the chaffinch breeding season compared with those found later in the year, as discussed in the previous section. Hence these webs are not as useful during the spring as they would be if they were at their largest sizes. The irregular webs of the Theridiidae did not appear to be regularly smaller during early spring than later, fitting in with the fact that members of this family generally over-winter as sub-adults.

Cribellate webs are spun by larger individuals, even the juveniles that predominate during the spring being larger than the adult araneids found at Garscube, and spinning webs whose size is less dependent upon the spider's size. The webs are continually added to, rather than replaced when their catching ability declines, as is the case in the ecribellate families (see section 3.5).

So, cribellate webs, probably spun by *Amaurobius*, are the second most abundant web type in this survey, and are of the largest size by a considerable margin during the chaffinch nest-building phase. Further, the number of cribellate webs is undergoing a rapid rise (see figure 6.40). Hence, on a basis of the amount of silk available to a chaffinch, there will be a strong bias for taking cribellate webs as a nesting material.

9.2.2) Cocoon silk

Little was learned from this study about the relative availabilities of cocoon types. The reasons for this are two-fold. Firstly, it is difficult to tell in the field to which spider group a cocoon belongs, since there is much variation within, and overlap between, families in cocoon structure (see section 3.5). Secondly, cocoons were found very infrequently during the spider silk survey (section 9.1.2).

There are, however, a few pieces of information which provide indications. Most cocoons collected for silk characterisation were from the araneid *Zygiella x-notata* (section 6.3.1). Some reasons for this are connected with the fact that the female can survive for a while after spinning the cocoon, as mentioned in section 8.2, but also this species was one of the commonest ones found (see section 6.4.1). Furthermore, these cocoons were less well hidden than those of other species. The family least commonly found in this survey was the Theridiidae. Non-web spinning families were not included in the survey.

It would therefore appear that cocoons from the Araneidae are at least more apparent at Garscube than those from other families.

9.3) RELATIVE SUITABILITY OF SILK TYPES DURING CHAFFINCH BREEDING SEASON

9.3.1) Web silk

I refer back to section 3.5 where I discussed the differences between the various web types in their possible roles as nesting materials. I suggested that the most suitable web-types would be the sheets of the Agelenidae and larger Linyphiidae, and the cribellate sheets. At the sites investigated at Garscube Estate, no agelenids were found, and only smaller linyphiids were present during the breeding season, as described above. That leaves the cribellate webs spun by *Amaurobius* as the best web silk available to the chaffinches. The reasons for its suitability can be summarised as the density and extensibility of the fibres, the persistence of the adhesive properties of the catching strands, and the visibility and accessibility of the silk, as well as the large extent of the web. This combination of features is not present in the orb, irregular and smaller sheet webs at Garscube. The properties of cribellate silk enable it to be used to greater advantage than the other web types, by the chaffinches, in the various binding roles described for web silk in section 7.2.

Orb webs may contain too little silk to be worthwhile collecting. Collection would inevitably mean the web collapsing around the chaffinch's beak, from where application to the nest would be tricky, and manipulation of the silk near impossible. It is also possible that some orb web silk is present in the nests, but so little, and the silk so fine, that it was not possible to find it. Exactly the same problems apply to irregular webs.

Ecribellate sheet webs again do not contain as much silk per unit area as the cribellate

webs of the Amaurobiidae. Furthermore, the silk is only slightly adhesive, if at all. Little is known of the other properties of this silk.

9.3.2) Cocoon silk

Again, I refer back to section 3.5, where I proposed that a range of families could provide cocoons suitable as nesting materials: some members of the Agelenidae, Theridiidae, Araneidae and Metidae could spin cocoons that would be useful. There structure would be advantageous in both the roles described in section 7.2, those of attaching lichen and binding the moss layer. The irregular, tangled mass of fibres which form at least part of all these cocoons would tie together these nest constituents.

9.4 SUMMARY OF FACTORS AFFECTING CHAFFINCH CHOICE OF SILK

From the information on the availability of the web types, and on their suitabilities described in this section, we expect to see a strong bias towards the use of amaurobiid web silk, rather than the others, in nests found at Garscube.

We have seen in section 8.1.1 that of the web silk taken from chaffinch nests and examined, all is cribellate. Unfortunately, we cannot discern whether this is a result of the greater availability of cribellate web during the nesting period, or its greater suitability. If more information about the dates of construction of the nests examined was available, we could investigate whether nests built later in the season, as replacements for earlier nests, also contain exclusively cribellate web silk, even though the amount of other types of silk in the environment during their building was greater. Nest 3 from Garscube was the last built, probably started after 7th May and before 8th June (see section 7.1). During this time, orb web numbers are approaching those of cribellate webs (figures 6.40 and 6.43), and the size of both orb and sheet webs increasing. Nevertheless, all the web silk was still

cribellate (section 8.1.1). This is a very good indication that it is cribellate web silk that is the most important of the webs available to the chaffinch because of the properties of the silk, rather than the abundance of the webs.

From the little information gleaned on availabilities and suitabilities of various cocoons, it would be reasonable to assume that those of the Metidae and Araneidae may present the best option for the birds to use in their nests, since they both appear to be available and suitable. We have seen in section 8.1.2 that araneid-type cocoons may be fairly common in chaffinch nests, compared with other, unidentifiable, cocoon silk. However, the certainty of all the information relating to cocoon usage is far less clear-cut than that for web usage.

CHAPTER 10

EFFECT OF SILK USE UPON CHAFFINCH BEHAVIOUR

10.1) EFFECT UPON THE METHODS USED IN SEARCHING FOR NEST MATERIALS

We can hypothesise that the search for nest materials may be governed by similar rules to the search for food, as has been studied by such authors as Tinbergen (1960) and Royama (1970). Silk may not easily be seen against all backgrounds, so finding suitable material may not be easy. We have see that collecting silk is a very important factor in determining the length of time taken to build a nest. This section deals with the forces that may dictate the methods employed in searching for web and cocoon silk.

10.1.1) Web collection

We have now seen that cribellate silk is probably both the most suitable and the most available web silk for the chaffinches to use in their nests.

If the birds search randomly for web silk, taking everything found, we would expect to find more cribellate web silk than other types. Alternatively a search image may be formed, in the manner of the foraging search image put forward by Tinbergen (1960), and the birds only see the commonest silk-type, or the most suitable - in either case, cribellate. In this way, web silk in nests may be expected to be almost exclusively cribellate. This would also be true if the birds see all web types but only take the largest and commonest since they require less searching effort (parallelling the foraging behaviour pattern

proposed by Royama, 1970)

We do see (section 8.1.1) that all web silk found in chaffinch nests was cribellate, and probably amaurobiid. We can therefore rule out the hypothesis that the birds take whatever web silk they find. It is therefore apparent that the birds in some way restrict themselves to only taking cribellate webs, though whether they form a search image or not is untested. In either case, both the efficiency of nest building, in terms of time spent, and the quality of the nest, are improved

If this silk is the most suitable, chaffinches should restrict their search to places where this silk is most easily found. We shall see what implications this may have for the area covered by the chaffinch territory in section 10.2.

10.1.2) Cocoon collection

Even with so few known cocoon silks and the problems with silk identification (section 8.2), we can still see the number of different cocoons used in each nest. Table 8.1 shows a summary of the cocoons present in each nest, giving the number of cocoons that appeared to belong to *Zygiella*, the number whose appearance suggested they may belong to other araneids, and the number that bore no resemblance to *Zygiella*. Of the 17 cocoons examined, from 5 nests, 11 appeared to be araneid, and 6 were indeterminate. Each of the indeterminate ones were different, and only two of the araneid type closely resembled *Zygiella*. Therefore, at least 8 different cocoon types were used, if all the other araneids were the same, and not more than 16, if all the araneids were different. Nest 1 contained 6 different types, but the other nests contained no more than three, with Nest 3 containing only one type of cocoon, and 12 units of it.

So generally, only a few different types of cocoon appear to be taken for each nest. This has implications for how chaffinches go about finding cocoon silk for their nests.

Collection of only a few cocoon types may be achieved in three ways. Firstly, chaffinches may restrict themselves to only a few kinds of the more accessible places, thus being limited to a small range of species, but take the cocoons present without discriminating. Secondly, they may only take the commonest cocoons from anywhere in the territory, with or without forming a forming a search image (see above). These first two possibilities would both reduce the search time for cocoons, compared with searching for a mixture of cocoons. The third alternative is that the birds restrict themselves to the most suitable cocoons, which would not necessarily be the most easily collectible. Forming a search image in this case would reduce the search time, though the most suitable cocoon would also have to be the most abundant for this time would be as short as for the first two possibilities.

The most common cocoon type found in nests is the one I describe as probably araneid. It may only be coincidence that this is also the cocoon type that I found most accessible during my survey at Garscube Estate (see Section 9.2.2). If it is not coincidence, then the most efficient search method would be to form a search image for the araneid cocoons. By limiting themselves to only a few locations, the chaffinches would reduce the number of araneid cocoons to which they have access, since araneids can spin cocoons in a variety of places.

The low number of different cocoon types in nests would support the idea that the birds need a specific range of cocoons with different properties in order to fulfil different roles. If any of these cocoon-types are uncommon, the search could be quite time-consuming. If more than one cocoon type can satisfy the same role, then a lack of one type would not make so much difference.

It is clear from the foregoing discussion, that the behaviour of chaffinches during the nesting period is very much affected by their need to find suitable silk to use in their nests, with only a limited time and energy budget.

10.2) SILK AVAILABILITY AND THE LOCATION OF CHAFFINCH TERRITORIES

Given that silk is often a very important nesting material, and that cribellate webs are the ones favoured for nest-building, as does appear to be the case from examination of nests (section 8.1.1), we can predict what type of sites will be important for a bird to include in the territory it defends. It should be borne in mind that a major function of a territory is thought to be to provide a good and secure supply of nesting materials, whereas food is often gathered from outside the boundaries (Newton 1972).

Yew trees were found to provide the best source of this silk amongst the sites studied in this work (section 6.4.2.2), and so we might expect chaffinches to include in their territory as many yew trees as are needed to supply all the webs required. Other trees with similarly rough and fissured bark may represent as good a resource - *Amaurobius* webs were also found on the bark of hawthorn and sycamore trees. Cribellate spiders also typically build their webs around crevices in walls and fences and around stones on the ground. Further amaurobiid webs were found on the carport (table 6.7), where the joints of the framework provided protection, and the frames themselves a suitable surface over which to spin the web. These would all be good elements to include in a territory.

Since we do not know which families' cocoons are favoured, we cannot draw the same inferences. However, if, as I suspect, araneid cocoons are often used, a chaffinch might be expected to include in its territory areas where araneids spin cocoons. Araneids occupy such a wide range of habitats (see, for example, Jones 1983), that this would not actually affect the chosen contents of the territory. This, together with the fact that there is no apparent regularity between nests in the cocoons they contain, makes it hard to believe from this study that cocoon availability may affect choice of where to breed, even though cocoon units considerably out-number web units in most nests.

The range of sites that are suitable for *Amaurobius* webs is quite wide and each of them

are quite common. Hence, as far as chaffinches are concerned, web availability will pose few restrictions upon where to breed. Likewise, araneid cocoons, the cocoon type I propose is most commonly used by chaffinches are widespread and common, if hidden. Hence, cocoon availability should not influence the chaffinches' choice of where to breed, except in very poor environments, where either the demand for the silk is considerable, or the availability very low. There are wider implications, however, for other passerine species, in other environments. The availability of suitable webs or cocoons, considering the apparent importance of these in many nests, as described in chapter 1, could have a very important bearing on the birds' decision on where to breed

So we can see that silk availability could potentially affect where a chaffinch decides to breed, and what area the territory should cover. We shall now see that silk availability may also affect the choice of when to breed.

10.3) SILK AVAILABILITY AND THE TIMING OF CHAFFINCH NESTING

Through natural selection, the timing of bird breeding should be adjusted so as to maximise lifetime reproductive success. In Britain, clutch size is normally 4 or 5 eggs each year (Newton 1964). Availability of food for the young is often cited as the key factor in selecting when to breed (e.g. Marler 1956). Eggs hatch when the number of defoliating caterpillars, the principal food of nestlings, is on the increase, so that when the chicks' demand for food is greatest, the amount of food available is high. Each stage of the breeding cycle is arranged so as to achieve hatching at the optimum time, within the bounds of the birds' ability to react to the relevant external factors. The stage of the reproductive cycle under consideration in this study is nest-building.

The ideal time to commence nest-building will be determined in part by the time required to complete the nest. If nest-building takes 8 days, and incubation takes 13 days,

then nest-building should commence around 21 days before the rapid spring rise in caterpillar numbers. The time taken to complete the nest will be affected in turn by the time at which the nest is built. This is because the availability, and hence time required for collection, of various materials will vary throughout the season. In the case of silk, the earlier in the season the nest is built, the less the amount of silk available, hence the longer the nest should take to build. The assertion by Marler (1956), that it is collection of cobwebs that slows construction, further emphasises this point.

The decision of when to build the nest is critical to the success of the nest. If the ideal time to build from the point of view of material availability, is not early enough for the eggs to hatch at the ideal time for food availability, the success of the nest will be sub-optimal. If too much effort is invested in the nest structure, by building when material availability is sub-optimal, clutch size may have to be reduced. We have seen in section 2.5 that the period of nest building makes high energy demands upon the female parent. Alternatively, the nest may be sub-optimal in terms of strength or camouflage due to inferior construction, by being completed in a short time span, thus running a greater risk of failing completely. Finally, the eggs may hatch too late to exploit maximally the defoliating caterpillars, and more young would die of, or be weakened by, starvation.

There is therefore a trade-off to be made in the decision on when to build.

It appears that nest construction took place at Garscube during the period late-April until mid-May. The amount of spider silk present in the environment at Garscube was very low until mid-April (Day 154 in figure 6.37). Then began a rapid rise in web numbers until the end of May (Day 192). This rise in cribellate webs, the only webs found to be used in chaffinch nests (see section 8.1.1), consisted of nearly tripling the mid-April low of 25 webs to a late-May peak of 70 (Days 154 to 192 in figure 6.40). This was, in fact, the highest number of cribellate webs found during the study for the whole year 1989-1990. So, from the point of view of the availability of suitable web silk, it would favour the birds

to delay nest-building as long as possible, up to the end of May. By the time the nest-building phase appeared to be finished at Garscube, cribellate web numbers had only doubled since the winter low, although that doubling mostly occurred between 16th and 27th April (Days 154 to 165), when nest-building was commencing (figure 6.40).

Cocoon numbers may play a greater role than web numbers in determining when to commence nesting. This type of silk is found in greater abundance in chaffinch nests. However, it appears from my data of silken structures found on the ceiling of the bicycle shed, that cocoon numbers are slightly lower between early-May and mid-July than earlier in the spring and later in the summer (see section 6.4.3). However, fluctuations in the number found are very small. The small drop during this period may of course be due to the cocoons being taken for use in birds' nests! Cocoons of spiders that are adult in the summer and autumn are designed to be persistent through the winter months, so numbers of these are never very low, and they should be available in early spring.

As we saw in section 6.4.3, during the nesting period (end of April to mid-May) only 2 new cocoons appeared, both on 18th May, which is probably after the chaffinch nests were completed. During the same period, 2 cocoons also disappeared, one on 27th April and one on 11th May. These may have been taken for use in nests, since there was no trace of them left behind, implying that they had not been destroyed as the spiderlings emerged. The spider species that spun these cocoons was not recorded. The highest turnover of cocoons occurred later in the summer, as described in section 9.1.2. So it would appear, that, like webs, cocoons are not as plentiful during the nest-building period as they are later.

These two pieces of information, that both webs and cocoons are not at high levels, may encourage chaffinches to commence nesting later, if the other constraints upon timing of nesting were to allow. When silk is more available, the duration of nest-building can be reduced.

The duration of nest-building by individual females at Garscube is not known, so no correlation between date of construction and duration of construction can be made. It does appear, though, that by delaying construction by two weeks, the amount of available web silk would be much higher (total web silk doubled between 27th April, when nest-building was first observed, and 11th May), and hence the time and energy devoted to nest-building would be reduced. By restricting the webs collected to cribellate sheets, this factor is reduced (the increase over the same period being by less than 25%). We saw in section 9.2.1 that cribellate webs may be chosen because of their greater abundance at this time, or because of their greater suitability. Assuming the birds are behaving optimally, other constraints on timing of breeding, especially the rise in numbers of defoliating caterpillars (the main food for chicks), may out-weigh those imposed by the change in silk availability. The time-savings by delaying the start of nest-building would have to be large enough to not delay the onset of egg-laying too much, or the energy savings large enough to allow a greater clutch-size. In this study it appears that a delay of a week would make little difference to the amount of cribellate silk available, since during this period there is little rise in web numbers (see figure 6.40). The savings of time and energy spent on silk collection would be small.

We do indeed see here the expected trade-off between the advantage of getting the nest built early to fully exploit the rise in defoliating caterpillars, and the disadvantage of taking a long time to build the nest because silk availability is low.

It is very possible that the lower number of cribellate webs earlier in the season could discourage the birds from building earlier. The number on 16th April (Day 154) was about half of the number counted ten days later (day 165) (figure 6.40). Hence, had nesting begun on 16th April, web collection could have taken twice as long.

This is evidence to support Marler's (1956) claim that silk collection is very time

consuming and a prime determinant of the length of the nest-building process. He provided no firm evidence, except for citing the observation that the two nests that took longest to build were built by first-year females who collected more silk than the others did. By providing evidence that nesting is delayed until the number of webs is rapidly increasing, and that further delay would save little time in construction, I can strongly support Marler's view. This all serves to highlight the importance of a study such as this when investigating the influences upon bird breeding success.

To decide if silk availability is more limited early in the season than later, it would be helpful to compare the number of silk units in early and late nests from one habitat. Unfortunately, dates of construction are known for too few nests.

Other factors will be important in determining when to build, such as higher visibility of the nest before the leaves on the tree or bush have developed. Nest-building does occur before the vegetation is in leaf, but by the time the eggs have hatched, the nests are well concealed by foliage. Weather conditions will play their part, either directly upon the birds or upon the emergence of defoliating caterpillars.

Silk availability at any site may vary from year to year. Whether or not the silk availability pattern observed for the year 1989-1990 is typical for Garscube Estate is unknown. So even if breeding success was heavily dependent upon silk availability, we should not necessarily expect timing of chaffinch breeding to be adjusted perfectly to the availability of silk. It can be envisaged though, from the foregoing discussion, that the number or success of territories in an area may be in part dependent upon the availability of silk, especially in those areas where the nature of the territory makes silk usage more important. For instance, with silk important in camouflage (see section 7.2), habitats where predator numbers are high, or foliage cover low, would gain more from the use of silk than habitats where the predation threat is low.

There can now be little doubt that when studying bird breeding, nest construction must not be ignored, especially were the use of silk is important. Silk availability may affect where to breed, when to breed, and potentially even clutch size.

CHAPTER 11

CONCLUSIONS

Silk is used in nests by passerines world-wide. The phenomenon has not been investigated in any detail previous to this study. Generally, very little attention has been paid to the adaptive significance of nest structure. But nest-building and nest structure are vital components of the breeding cycle of any bird. If the nest fails, a whole year's reproductive effort can be wasted. Less dramatically, if the nest is in anyway sub-optimal, reproductive success can be reduced. The wide-spread use of silk is an indication of the importance of this material in a variety of different nest structures. Silk evidently must be a versatile and widely-used nesting material, and it is therefore a very important to understand, for the purposes of looking at the importance of the role of the nest in breeding, why and how silk is used, and the types of silk involved.

This study has investigated the phenomenon in detail for one European passerine species - the chaffinch. Four questions were posed in chapter 1. I shall consider the answer to each in turn, and then look at some wider implications of the study.

11.1) WHAT MAKES SPIDER SILK SUCH A WIDESPREAD NESTING MATERIAL?

Silk is a fibrous protein secreted by special glands in an arthropod to the outside of the animal (section 3.2). The order of arthropods that exploit silk to the fullest is the Aranea - spiders. Spiders use silk as its building material, constructing from it a variety of objects, ranging from single supporting threads to large 3-dimensional cocoons (see table 3.2).

In the environment there is a range of structures with different properties, which can

potentially be used by another animal. In birds, we can see that a wide range of species can use these artifacts in producing their own structures (see Chapter 1). The primary sources of silk we might expect to be used are cocoons, dense webs and retreats. The large number of spider families and species serves to create further choice for birds (section 3.5), perhaps enabling them to use the specific structures that are best suited to the jobs.

Each spider can produce several different types of silk. These can be used in combination, to produce the variety of structures. The silk from each type of gland in a spider has different properties. Precisely which glands produce which silks and what these are used for is still debated, but I present a likely picture in table 3.3.

The properties of silk fibres have been studied in detail. They have a high tensile strength, ranging from 0.4 to 1.7 GNm^{-2}, depending upon the type of silk and the conditions under which it is measured (see table 3.4). These values are higher than for nylon, and the tensile strength of steel is at the lower end of this range (Gordon 1978).

Silk is highly extensible. Figures given in the literature range between 25 and 300% breaking extensions, again depending upon the type of silk and conditions under which measurements are made (table 3.4). These values are greater than for both nylon and steel (Lucas 1964, Gordon 1978).

The actual breaking strain for a thread of silk depends upon the diameter. Spiders often spin threads consisting of bundles of several fibres thus strengthening them (see section 3.4.1). Generally, larger spiders produce coarser threads (section 3.4.1.1).

In addition to the strength and extensibility of silk, some fibre-types have adhesive properties (section 3.4.2). These may be exploited by birds, depending on how persistent the adhesion is. The glue-like secretions from silk glands of some ecribellate spiders tend to be water soluble, while the adhesive properties of cribellate spiders' catching threads

appear to be more persistent, relying on entanglement by fine fibrils (section 3.4.2). As we have seen, it is the latter type of web silk that is strongly preferred by chaffinches as a nesting material (see section 8.1).

Structures made from silk are therefore generally strong, flexible, and extensible, due both to the properties of the silk fibres and the way they are constructed. Further, web silk represents a renewable resource (section 3.4.2).

The structures built by spiders of different families can differ in certain respects, containing as they do different types of silks in different proportions. I concluded in section 3.5 that the most suitable webs would be those of the families Agelenidae, Linyphiidae and Amaurobiidae, since they provide large dense mats of silk which are easily collected and possess properties appropriate for binding nests.

Cocoons would be best from certain members of the families Araneidae, Metidae, Agelenidae and Theridiidae, since they are large, thick and consist of a variety of layers. Coloured cocoons from a variety of families may also offer opportunities for camouflaging the nest (section 3.5).

The importance of the specific properties of silk is borne out by the fact that cocoon silk can not be replaced by animal wool, even though the properties of the two materials are very similar, and wool is coarser and hence stronger (see section 7.2), and in spite of wool often being abundant in nests.

So we see that the unique properties of silk, plus the variety of silks and structures available, mean that it is a highly useful and versatile material for birds to use for their nests as a structural, binding and securing material, and potentially as camouflage.

11.2) HOW IS SILK USED IN THE NESTS OF CHAFFINCHES?

The basic structure of chaffinch nests is constant (see section 2.1). The layers are, working from the outside inwards: (A) a superficial layer acting as a camouflage, the extent of which is variable; (B) a foundation layer and rim, (C) an inner layer, (D) the lining of hair, feathers etc. Silk was found in Layers A, B and C, though very little in found in C (section 7.2). The composition of Layers A and B shows great variation. Many different materials can be used in the camouflage, and the structural foundation, though composed mostly of moss, can be augmented by a range of materials, including wool, hair and small twigs (section 7.1).

I conclude tentatively that in most cases, a simple structure appears to be favoured, composed of only a few different materials. The simplest, and possibly ideal, structure is that described above, with Layer A being composed of lichen, held on by cocoon and web silk, Layer B consisting of moss and grass, with some web or cocoon silk reinforcing the structure, and Layer C containing only moss (see section 7.1). However the habitat in which the chaffinch is breeding determines what materials are available and the need to provide a different camouflage where the surrounding vegetation is unusual, may necessitate the use of other materials.

The uses of silk discerned in this study of chaffinch nests are as follows:

i) Holding on materials such as lichen, twigs, and bark in Layer A.

ii) Binding the moss of Layer B, and incorporating other structural materials, such as rootlets into this Layer;

iii) Attaching the nest to the bush or tree;

iv) Camouflaging the nest (possibly).

Cocoons are used in the more specific functions of attaching lichen and "embedded in Layer B" (where they may act as additional camouflage or reinforce the structure), while web appears to be a more versatile binding material. Web silk is far less common in chaffinch nests in general, in spite of their greater apparency in the environment (section 9.1.4), implying that cocoon silk is more suitable for these roles and worth the extra search time.

So it appears that by being able to use silk in several different ways, chaffinches are able to build nests in environments where the materials available are not ideal. Without the extraordinary properties of silk, chaffinch breeding may well be greatly restricted.

11.3) WHAT TYPES OF SILK ARE USED BY CHAFFINCHES?

All the web silk found in the 5 nests examined was cribellate (section 8.1), and probably from *Amaurobius*, since this was the only cribellate spider found at Garscube (section 9.1.1.4). However, since *Amaurobius* was the only one found, the appearance of other cribellate webs under SEM is not known.

We have seen that this silk is the most abundant at Garscube during the nesting period (section 9.2.1), as well as apparently one of the most suitable (section 9.3.1).

Cocoon silk poses more problems, for the reasons discussed in section 8.2. However, it does appear that a large proportion of cocoons from nests may be from members of the Araneidae.

I have proposed in section 10.1 that in order to reduce search time, it may be most efficient to form a search image for the most suitable silk, if it is also relatively abundant. Cribellate webs satisfy the criteria. By restricting the search to areas where this silk is most

easily found - e.g. rough bark on trees, brick walls - search time will be reduced further.

It is unclear what types of cocoon are available at Garscube during the nesting period (section 9.2.2), and the search method employed is not predictable from this study.

11.4) COULD SILK AVAILABILITY LIMIT THE TIME OR PLACE OF NESTING?

Since chaffinches appear to use web silk from only cribellate spiders in their nests (section 8.1.1), they would be expected to include many sites suitable for cribellate webs in their territories. Since the types of places *Amaurobius* spins are quite numerous and common, including some types of tree bark, fences, walls and other crevices, the number of areas ruled out would be few.

The lack of identification of cocoon silk makes it harder to assess whether this silk type could affect the distribution of territories. However, I suspect that araneid cocoons are often used (section 8.1.2), and this family can live in a very wide range of habitats (section 3.1). Providing all araneids are equally useful in this respect, availability would not greatly affect the choice of where to breed.

The low number of cribellate webs present in the environment prior to the onset of nest-building (see figure 6.40) may discourage the chaffinches from building earlier, but since the rise of cribellate web numbers is only moderate in the month after the onset of nest-building, little advantage in terms of time and energy savings will be gained the chaffinches by delaying.

The amount of cocoon silk present in the environment appears from this study to vary little throughout the spring months, and so should not affect the decision on when to

breed.

Though silk availability is not optimal during the nest-building period, the need for the chicks to be hatched in time for the rapid spring rise in defoliating caterpillars, the chicks major food source, is the overwhelming constraint on delaying nest-building.

The precise balance of forces varies form habitat to habitat and from year to year. Therefore, we cannot expect chaffinches to behave optimally, either through adaptation or adaptability.

11.5) IMPROVEMENTS AND EXTENSIONS TO THE METHODS

There are several ways that this study could be improved to clarify some of the points arising from the conclusions I have been able to draw about the way in which chaffinches use silk in their nests and the consequences of this upon chaffinch breeding.

11.5.1) Information on the nests examined

More detailed information on the nests examined could provide stronger indications as to the importance of silk. If the habitat structure is better known, perhaps with some form of diversity index, it would be possible to look for correlations with nest composition. It could be discovered what types of habitat do not necessitate silk in their nests, and what types require the highest amounts.

Likewise, the breeding success of nests may show correlations with silk content, when the materials that require silk are taken into account, if the data set is large enough. No information on breeding success was available for any of the nests in this study, except that all the Garscube nests failed.

One important feature of chaffinch nests on which information was not always available, was how it was attached to the supporting plant. Whether the foundation of the nest was built around twigs or if the nest was placed in a crux and held in place by silk is not known for the majority of cases. At least one nest was suspended by silk from twigs around the rim.

11.5.2) Silk identification

Without a more extensive range of silk in the library of silk spun by known spider species and available for examination under light and scanning-electron microscopes, it will be impossible to be any clearer about what types of silk are used in chaffinch nests. In particular, more types of cocoon silk need to be examined. From a larger range of species, patterns within families may be discernible, enabling identification to family or genus even if silk found in nests does not closely resemble any of the silk in the library.

To be certain about the identification of web silk, ascribed to the genus *Amaurobius* by default, silk from a wider range of cribellate spiders would have to be available. Chaffinches from areas other than Garscube Estate may have different species available to them, and even the chaffinches at Garscube may have found supplies of cribellate silk spun by a different family that I could not find.

Hence more thorough searching for silk with the spider present at Garscube would have been useful, if very time-consuming. Ideally, spiders from the whole of Britain would have their silk examined and characterised, and a fauna list for the area from which each chaffinch nest examined originated should be available. To create an accurate library of silk by rearing spiders would entail keeping each species separate, in containers large enough not to affect the spiders' spinning behaviour (eg see Reed et al. 1970).

Other techniques could be employed in characterising silk, than just microscopic examination. The possibility of using infra-red spectroscopy to analyse the silk was

investigated. It may be useful only if the silk samples could be cleaned and purified, and the silk samples dried so that they contain the same amount of water. The sensitivity of the analysis would have to be rather high, bearing in mind the consistency of the amino-acid compositions of one type of silk from different families of spider. Also, we have seen much disagreement in the literature in the composition of one silk from the same species.

The spectroscopy would be carried out on samples of web of cocoon silk, which contain more than one silk type. The combination of silks used does differ between families, in the case of webs, and possibly genera in the case of cocoons, and these differences may show up in the analysis.

Any techniques which involve biochemical analysis of silk would be fraught with the same problems of purity of the samples and inconsistencies within species and overlap between unrelated species. Amino-acid analysis would have to be carried out on individual fibres rather than whole units of structures, since the combinations of different silk types in the same analysis probably would blur the differences between species. The separation of individual fibres would need to be done by eye, and it would be very difficult to achieve reliability, and very time consuming.

If identification of cocoons could be improved, it could be investigated whether different cocoon types are used for different purposes by the birds. Even without firm identification, qualitatively different structures could be investigated in this way, but even for this, some form of categorisation of structures would be needed, which is not possible without a wider range of cocoons available to classify.

The chaffinch has been seen destroying the silk tents of pine caterpillars in France (Cugnasse 1987). Such behaviour in other birds was thought to be in order to obtain the caterpillars as food. However, Cugnasse suggests that since the caterpillars are noxious, and the activity is seen during the reproductive period, that the behaviour is in fact nest

material collection. If this is the case, then a geographically wider study of the use of silk in chaffinch nests must include investigations as to the availability of caterpillar silk, and a comparison of the silk from nests in regions where such tents are frequent with silk from the tents. If this silk is used in nests, comparing its role with spider web and cocoon silk may provide important extra information on silk use in general.

11.5.3) Silk survey methods

The methods used to survey the availability of silk types were adequate for this study, in that cribellate webs were the only ones found in nests, and identification of cocoons in nests was difficult anyway. However for a more detailed investigation, over a longer time period, improvements could be made.

Firstly, distinguishing between web types in the field was occasionally unreliable. From a distance, sparse cribellate sheets can be confused with the denser ecribellate irregular webs (family Theridiidae), and the irregular webs that contained a form of sheet could occasionally be taken for a genuine sheet web of the Linyphiidae.

To include more sites in a survey like this one would improve the accuracy of the picture it creates, though the sites chosen did provide a good cross-section. Extra sites should include the types of places cocoons would be found, and so be less visible. Such a search would inevitably be more time consuming, but a better picture of the fluctuations of cocoon numbers may be formed. From it we could say whether or no it is likely that birds may be limited in time or space in their nesting.

More useful still would be an ability to distinguish between various cocoon types in the field, and compare the abundance of each type. This would help show whether the birds are choosing particular types of cocoon for their nests.

Finally, continuing the survey over several years would reveal how well adapted the birds are in terms of timing of breeding to the expected availability of silk.

None of these improvements is within the scope of this project.

11.5.4) Investigations into chaffinch behaviour

By carrying out choice experiments on captive birds, where the nesting materials available are controlled, it would be possible to see if the types of silk chosen are indeed influenced by the other nesting materials.

I have proposed that chaffinches choose exclusively cribellate web silk, but a variety of cocoon silk. Choice experiments could show whether, if the amount of cribellate silk available is small, chaffinches make do with a less suitable silk. Furthermore, we could see if the chaffinches select the cocoons they use, or simply take whatever is available.

11.5.5) Summary

It is clear therefore that from the work so far carried out on this subject, many questions have arisen, and the scope for further research into the relationship between nest architecture and silk content is considerable. Ultimately, similar investigations should be carried out on a variety of bird species, to see how consistent the patterns are.

11.6) WIDER IMPLICATIONS OF THIS STUDY - OTHER BIRDS

We have seen the range of properties possessed by spider silk and the possibilities it offers as a nesting material. In chaffinch nests we have seen cribellate web silk as a multi-purpose binding and sticking material, and cocoon silk as a less versatile material,

attaching lichen and holding the moss layer together. It is likely that this range of functions of silk is also found in similar nests built by other birds from the same region, such as the goldfinch, ... A moss or grass structure may be inherently weak without silk. We see the grass cup of muscicapid fantails is completely bound round with spider silk. Further, materials attached to the outside of nests will always be more firmly secured by the addition of suitable silk.

However, the full range of functions of silk appear not to be exploited by chaffinches. We have seen in chapter 1 that many tailor birds use silk to stitch leaves together, that spiderhunters use silk as rivets punched through leaves, and that *Terpsiphone* spp use papery cocoons to decorate or camouflage the outside of their nests. Pendulous nests are often attached to overhanging vegetation by means of spider silk alone (*e.g.* rock warblers). This allows birds such as hummingbirds to build at the extreme edge of trees, to avoid predation (Hansell 1984).

I suspect that the chaffinch does not exploit fully the properties of the silk available to it, since the long-tailed tit, by using silk extensively, produces a strong, flexible and resistant bag-like nest, but breeds in similar areas to the chaffinch. Therefore, I expect that several different nest designs in the same region will also use silk, but in rather a different manner to the chaffinch.

The ability to use silk in these ways depends upon the properties of the silk available. Birds from other regions of the world have available to them silks and silken structures not present to birds in Northern Europe. Even birds in southern Britain will have access to silk from spider species not present at Garscube Estate. Cribellate web silk is used by chaffinches as a multi-purpose material, and it is likely that it is also used predominantly by many other birds, from other parts of the world. Their is some evidence from photographs of a range of tropical nests that silk with an appearance very close to the webs found in chaffinch nests, is commonly present. To examine such silk microscopically

would be extremely interesting.

However, tropical birds will also have available silk from large ecribellate spiders. I would expect silk from the araneid *Nephila* spp that spin giant golden orbs to be used where the sticky properties of the glue-like droplets are particularly important. Sources of such silk, which is far coarse and stronger than from temperate araneids, would be particularly plentiful if like *Zygiella* (Leborgne and Pasquet 1987), *Nephila* tend to congregate by finding silk spun by conspecifics.

Birds form other regions of the world may be able to use silk from not only webs and cocoons, but also others of those spider silk structures listed in table 3.2. The larger tropical spiders may spin large enough moulting chambers, spiderling nurseries, swathing bands, or even attachment discs, to be of use to the smaller passerines, such as hummingbirds. These structures will have their own properties, giving them the possibility of being used in different roles.

Furthermore, silk from arthropods other than spiders may be available for use in nests. For instance, silk from caterpillars, such as tent caterpillars or silkworms, is more plentiful in warmer regions. The properties of these silks, apart from the silkworm *Bombyx mori*, has not been studied, but would be expected to be rather different from spider silk, and so perhaps used in different ways.

The ability of birds to visually differentiate between silk types is of course an important factor when considering what types of silk are used in nests and the differences between the roles of these silks. Differentiating between ecribellate sheets of the Linyphiidae and cribellate sheets of the Amaurobiidae can be difficult, though the location an orientation of the webs could be used as a guide. Within families, the differences between species or genera often may not be perceivable, though for a bird to have a preference for one over another, the implied differences in properties may be

manifested in the appearance of the structures.

I have shown that in temperate areas, where the availability of suitable silk is variable through the year, that nest-building may be constrained in time and/or space. This problem would not be limited to chaffinches, and it can be imagined that the those birds that use silk to a greater extent will be more affected. However, in the tropics, spider activity is not seasonal, and so timing of breeding can be better tuned to other environmental influences.

There is apparently an upper limit to the size of bird that can use silk. In order to hold a very heavy clutch of eggs, the silk would have to be either very strong or be used in such vast quantities that collecting it all would be unreasonably time-consuming. In larger birds, whether the attachment between the nest and its base could consist of web silk, as it can in the chaffinch, is not known, though Hansell (1984) finds no accounts of non-passerine birds or larger passerines such as corvids using silk in any way, and further investigation for this study also failed to show any examples. The nest architecture is very dependent upon the size of the bird that builds it, as a large bird needs a stronger nest. The cup style probably has engineering constraints on size and strength, so larger birds build different styles. These, being constructed on different principles, may not need silk at all as a nesting material, its properties offering nothing that can be exploited. For instance, a rigid nest like the stick platform of corvids and pigeons will not need the extensibility of a material such as silk to hold it together. Indeed, such a material may be disadvantageous, weakening the structure.

Another size constraint upon the use of silk would be the ability to collect the material. Webs are often spun in small spaces, amongst foliage or on tree bark. Larger birds would have difficulty gaining access to these places, finding suitable perches within reach of the silk, and balancing at the right angle to collect the silk.

So this study has provided some answers to the questions posed on silk use, and raised implications about the ways in which silk is used by other birds, the limits on its use, and the limits imposed by its use, as well as the widening of the range of possible nest designs and the range of nest locations.

11.7) RELATIONSHIP BETWEEN SILK IN NESTS AND WEBS AS A FOOD SOURCE

It has been proposed in the literature that there may be a connection between the use of spider silk as a nesting material and the stealing of prey items by the bird from the spiders web. There are accounts of birds from 7 passerine families and piciform feeding from webs (see table 11.1). All but two of these families also contain members which use silk in their nests. The exceptions are the waxwings (Bombycillidae), and the woodpeckers (Picidae). Brockman and Barnard (1979) suggest web collection provided the behaviour patterns for cleptoparasitism. However, Waide and Hailman (1977) contrast the behaviour patterns used by a blue bunting (Fringillidae) taking prey from webs, and gathering webs as nest material. Furthermore, in all cases where the type of web involved is stated, it is an orb. We have seen that its use as a nesting material appears to be limited, at least outside the tropics. In one case, the spider species is given - *Nephila clavipes*. It is the large, thick stranded orbs of this genus that I have proposed as being the most useful orb webs available world-wide. The connection between feeding from and collecting webs seems tenuous.

Table 11.1 The examples in the literature of birds feeding from spider webs.

ORDER
Family
Species

Common Name	Scientific name	Web type	Reference
PICIFORMES			
Picidae			
Downy woodpecker	*Picoides pubescens*	Orb	a
PASSERIFORMES			
Bombycillidae			
Cedar waxwing	*Bombycilla cedrorum*	Vertically-orientated	b
Parulidae			
Prairie warbler	*Dendroica discolor*	Orb of *Nephila* sp	c
Yellow-rumped warbler	*Dendroica coronata*	Vertically-orientated	d
Trochilidae			
Fawn-breasted hummingbird	*Amazilia yucatanensis*	Vertically-orientated	d
Fringillidae			
Blue bunting	*Cyanocompsa parellina*	Orb	d
Troglodytidae			
White-bellied wren	*Uropsila leucogastra*	?	d
Vireonidae			
Yellow-green vireo	*Vireo flavoviridis*	?	d

References:
(a) Tiebout (1986)
(b) Burt *et al.* (1976)
(c) Douglass (1977)
(d) Waide and Hailman (1977)

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APPENDIX A

DETAILS OF THE NESTS EXAMINED

The 38 nests examined. For each nest the location, habitat, the tree or bush in which it was built, and the date are given, if known. A checklist of materials present in each nest is also given, with the number of pieces of those materials that were counted shown in brackets.

'Wool' refers to animal wool and man-made cotton wool, but not any natural plant fibres, which are given their own categories.

'Other silk' refers to silk that could not be identified with certainty as spider web or cocoon.

** indicates that the material was very plentiful, forming a major structural component of the nest.

NEST No.	1	2	3	4	5
LOCATION	Garscube Estate	Garscube Estate	Garscube Estate	Garscube Estate	Central Scotland
HABITAT	Parkland	Parkland	Parkland	Parkland	unknown
TREE/BUSH	unknown	beech	rhododen-dron	yew	unknown
DATE	Mar 1988	May 1990	June 1990	June 1990	Sept 1989
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+		+	+
Lichen	+ (124)	+ (19)	+ (89)	+ (40)	+ (4)
Rootlets	+	+		+	
Leaves	+				+
Wool	+ (5)	+ (8)	+ (3)		+ (4)
Twigs	+ (7)	+ (9)	+ (11)	+ (1)	+ (6)
Feathers	+				
Plant Down	+				+
Paper/Tissue		+ (10)			+ (12)
Bark		+ (2)	+ (6)	+ (4)	+ (1)
Woody fibre			+	+	
Hair				+	+
Leaflets					
Wood strips					
Wood					
Seeds					
String					
Skin					
Fabric					
Web Silk	+ (46)	+ (9)	+ (42)	+ (26)	+ (5)
Cocoon Silk	+ (31)	+ (23)	+ (71)	+ (56)	+ (19)
Other Silk	+ (4)				+ (5)

NEST No.	6	7	8	9	10
LOCATION	Central Scotland	City of Glasgow	Glasgow area	Glasgow area	Glasgow area
HABITAT	unknown	Parkland	Village garden	Village garden	Parkland
TREE/BUSH	unknown	Conifer	Ivy bush	Ivy bush	unknown
DATE	Sept 1989	Sept 1989	Oct 1989	Oct 1989	Oct 1989
MATERIALS					
Moss	+	+	+	+	+
Grass	+		+	+	+
Lichen			+	+	
Rootlets					
Leaves	+		+		
Wool	+ (2)	+ (**)	+ (8)		
Twigs	+	+ (**)	+ (6)	+ (4)	+ (5)
Feathers	+			+	+
Plant Down				+	+
Paper/Tissue	+ (13)				
Bark	+ (5)	+ (1)			+ (4)
Woody fibre					
Hair	+				
Leaflets		+ (20)			
Wood strips					
Wood					
Seeds					
String					
Skin					
Fabric					
Web Silk		+ (21)	+ (18)	+ (35)	+ (4)
Cocoon Silk	+ (6)	+ (34)	+ (1)		+ (1)
Other Silk		+ (1)	+ (1)		+ (1)

NEST No.	11	12	13	14	15
LOCATION	W.Lothian Scotland	Edinburgh	M.Lothian Scotland	Ayrshire	Ayrshire
HABITAT	Country garden	unknown	Country garden	unknown	unknown
TREE/BUSH	Honey-suckle	unknown	Snow-berry	unknown	unknown
DATE	June 1973	1928	June 1968	May 1877	May 1877
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+	+	+	+
Lichen		+ (86)	+ (375)	+ (450)	+ (180)
Rootlets		+			
Leaves					
Wool	+ (16)	+ **	+ (11)		+ (7)
Twigs	+ (10)	+ (5)		+ (4)	+ (3)
Feathers	+	+			+
Plant Down					
Paper/Tissue			+ (6)		
Bark				+ (14)	
Woody fibre					
Hair				+	+
Leaflets					
Wood strips	+ (60)				
Wood			+ (3)		+ (1)
Seeds				+ (4)	+ (7)
String					
Skin					
Fabric					
Web Silk	+ (21)		+ (60)		
Cocoon Silk	+ (1)	+ (28)	+ (30)	+ (196)	+ (53)
Other Silk	+ (2)		+ (2)		

NEST No.	16	17	18	19	20
LOCATION	Possil Glasgow	Isle of Arran	unknown	unknown	Glasgow area
HABITAT	Marshland	Highland	unknown	unknown	unknown
TREE/BUSH	unknown	unknown	unknown	unknown	unknown
DATE	May 1877	unknown	unknown	unknown	unknown
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+		+	+
Lichen	+ (76)	+ (52)	+ (44)		+ (77)
Rootlets	+		+		
Leaves					
Wool	+ (14)	+ (3)	+ **	+ (1)	+ (11)
Twigs	+ (7)		+ (3)	+ (1)	+ (2)
Feathers	+		+		+
Plant Down	+				
Paper/Tissue					
Bark		+ (2)		+ (5)	+ (4)
Woody fibre					
Hair	+		+		+
Leaflets					
Wood strips		+ (45)	+ (11)		
Wood				+ **	+ (4)
Seeds	+ (1)				
String					
Skin					
Fabric					
Web Silk	+ (5)		+ (4)		+ (16)
Cocoon Silk	+ (44)	+ (44)	+ (1)	+ (162)	+ (35)
Other Silk					

NEST No.	21	22	23	24	25
LOCATION	unknown	Berkshire Downs	Northum-berland	Northum-berland	E. Yorks
HABITAT	Parkland	Farmland	Moorland	Garden	Rural garden
TREE/BUSH	unknown	Hawthorn	unknown	unknown	Apple tree
DATE	1980	Dec 1989	Dec 1989	Jan 1990	Jan 1990
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+	+	+	+
Lichen	+ (21)	+ (26)	+ (48)	+ (1)	
Rootlets	+				+
Leaves		+		+	+
Wool	+ (8)		+ (7)	+ (12)	
Twigs	+ (17)	+ (6)	+ (1)	+ (1)	+ (5)
Feathers			+	+	+
Plant Down					
Paper/Tissue		+ (31)			
Bark	+ (15)	+ (3)	+ (9)	+ (2)	+ (1)
Woody fibre					
Hair	+				
Leaflets				+	
Wood strips					
Wood					
Seeds					+ (1)
String					
Skin					
Fabric					
Web Silk		+ (8)	+ (24)	+ (11)	
Cocoon Silk	+ (58)	+ (45)	+ (18)	+ (2)	
Other Silk			+ (2)		

NEST No.	26	27	28	29	30
LOCATION	Cheshire	W. Yorks	Powys, mid-Wales	Oxford-shire	Oxford-shire
HABITAT	Village garden	Deciduous woodland	Garden/ Farmland	Pear orchard	Pear orchard
TREE/BUSH	Hawthorn hedge	Rhodo-dendron	unknown	Pear tree	Pear tree
DATE	Jan 1990	Jan 1990	Jan 1990	Feb 1990	Feb 1990
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+	+	+	+
Lichen		+ (25)	+ (42)	+ (4)	
Rootlets				+	+
Leaves	+				+
Wool		+ (3)	+ (8)	+ (4)	
Twigs	+ (5)	+ (1)	+ (8)		+ (5)
Feathers	+	+		+	+
Plant Down				+	
Paper/Tissue	+ (1)		+ (6)		
Bark		+ (9)	+ (2)	+ (3)	
Woody fibre					
Hair			+		
Leaflets					
Wood strips	+ (19)				
Wood					
Seeds					
String	+				
Skin					
Fabric					
Web Silk	+ (17)	+ (7)	+ (2)	+ (4)	
Cocoon Silk	+ (8)	+ (3)	+ (35)	+ (31)	
Other Silk	+ (2)		+ (1)		

NEST No.	31	32	33	34	35
LOCATION	Oxford-shire	Gywynedd, N. Wales	Argyle	N Ireland	Devon
HABITAT	Pear orchard	Wooded Garden	unknown	Suburban garden	Moorland
TREE/BUSH	Pear tree	Vibernum	unknown	Cypress tree	Gorse bush
DATE	Feb 1990	June 1989	Apr 1990	1989	1989/90
MATERIALS					
Moss	+	+	+	+	+
Grass	+	+			
Lichen			+ (39)		+ (3)
Rootlets	+				
Leaves					
Wool	+ (6)	+ (5)	+ **	+ (7)	+ **
Twigs	+ (5)	+ (1)	+ (8)		+ (33)
Feathers	+	+	+	+	
Plant Down					
Paper/Tissue					
Bark		+ (2)	+ (3)		
Woody fibre					
Hair	+	+			
Leaflets				+ (40)	
Wood strips				+ **	+ (44)
Wood	+ (8)				
Seeds		+ (2)			
String				+	
Skin	+				
Fabric				+	
Web Silk	+ (5)	+ (24)	+ (1)	+ (40)	
Cocoon Silk		+ (14)	+ (12)	+ (9)	
Other Silk		+ (3)			

NEST No.	36	37	38
LOCATION	Devon	Devon	Devon
HABITAT	Scrubland	Rural garden	Scrubland
TREE/BUSH	unknown	unknown	unknown
DATE	1990	1989/90	1989
MATERIALS			
Moss	+	+	+
Grass			
Lichen	+ (5)		+ (28)
Rootlets	+		
Leaves			
Wool	+ (17)	+ **	+ (3)
Twigs	+ (1)	+ (10)	+ **
Feathers			
Plant Down			
Paper/Tissue			
Bark			
Woody fibre		+	
Hair			+
Leaflets			
Wood strips	+		
Wood			
Seeds			
String			
Skin			
Fabric			+
Web Silk		+ (9)	+ (4)
Cocoon Silk	+ (9)	+ (4)	+ (5)
Other Silk			

APPENDIX B

ECOLOGY OF THE SPIDERS FOUND AT GARSCUBE

Fourteen different species of spider were found at Garscube in the period October 1989 to June 1990, from 5 web-building families. I here briefly describe the ecology of the spiders involved. The information is taken from Jones (1983) Bristowe (1958) and Nielsen (1931). Nomenclature follows that of Jones (1983).

This list is not intended to include all the spider species present at Garscube Estate, but it is hoped that it contains all the species whose silken structures can be spotted and removed by small birds.

THERIDIIDAE

Steatoda bipunctata (Linneaus)

This species is common throughout Britain, usually found in and around houses, but occasionally on trunks of conifers and fences. The females can live up to four years. It is a Theridiid that builds a sparse sheet web with viscid mooring threads to trap crawling insects. The eggs, numbering 100-150 in number, are wrapped sparingly in silk, but the web is drawn across the cocoon, which is placed against a wall or bark. The spider matures in the autumn.

My single specimen was an adult female found inside a brick bicycle shed, amongst the eaves. Its web and retreat-cum-cocoon were all found together on October 4th 1989.

Theridion varians Hahn

Again common and widespread throughout Britain, it is found chiefly on trees, bushes, fences and the like, the irregular web being placed in corners and the angles of branches. The threads can be viscid. They reach maturity in early summer, though the females may live until autumn. The cocoon is a globe of white silk concealed in the angle of the branches or on the underside of a leaf and guarded by the female. The retreat, which will contain the cocoon, is an inverted cup of silk.

A single specimen, an adult female, was found in its web on the outside wall of the bicycle shed on May 11th 1990. The retreat was not located.

Theridion melanurum Hahn

In its irregular web on the outside of buildings, this species is commonly seen in southern Britain, but is rare in Scotland. It will also build on trees with deeply furrowed bark. It matures in early summer, when it builds a cocoon consisting of a thin layer of silk over greyish eggs. After they hatch, the juveniles overwinter inside buildings (Kirchner 1987).

A single, adult male specimen was found near to the female *T. varians*, and on the same date, on its own web.

Theridion pallens Blackwall

Common and widespread in Britain in the foliage of trees and among low plants, the web is strung between twigs. It matures in early summer, with the adult females often found throughout winter, though the overwintering stage is generally the subadult (Kirchner 1987). The white egg sac, which is far larger than the spider, is placed on the underside of leaves and has sharp projections pointing in one direction. Around 50 eggs may be found in each cocoon.

A male sub-adult was found on November 1st 1989 on the trunk of a beech tree in its

web.

METIDAE

Meta segmentata (Clerck)

A usually rather small orb web is spun up to 1.5 m high in woods, gardens and wasteland. This is another species that is abundant throughout Britain. the spider lives in the open hub of the web, building no retreat. when off the web, it waits on a twig with a pair of legs touching a signal thread. It matures in late summer or autumn, but occasionally in spring (some believe this population to belong to a separate sub-species), and the female lays her eggs in the autumn, and dies soon afterwards. The cocoon is about 7 mm in diameter, a globular pale yellow mass, placed beneath stones or fallen leaves. The eggs hatch the following spring.

Several male and female specimens of *M. segmentata* were found on a holly hedge on September 21st 1989, and a further female found with its web spun between two twigs of a small shrub. All were adults.

ARANEIDAE

Araneus diadematus Clerck

Again widespread and common, the large orb web (up to 40 cm in diameter) of the garden spider is found between 1.5 and 2.5 m above the ground in woods, gardens and heathlands. The web has a closed hub, and usually a retreat is built, connected by the signal thread, in a rolled leaf or crevice. It matures in late summer to autumn. the female lays 300 - 800 yellow eggs, which are cemented together, in September or October beneath loose bark or in crevices on houses and fences *etc.*, and a dense yellow hemispherical cocoon spun about them. This may be camouflaged with small loose objects in the vicinity such as small splinters of wood or leaves. A dense white web is spun over the whole and fixed to the underlying surface all around. The eggs hatch in the following

spring,and the young emerge in June-July. They grow through the summer and autumn, then spend winter in a state of torpor, and continue to mature during their second spring. They mate and die during their second autumn.

Juveniles were found on the holly hedge both on 21st September 1989 and 3rd May 1990.

Zygiella x-notata (Clerck)

The orb web of this species is easily identified on window frames and fences, and bushes in the close vicinity of houses. The orb has a missing segment where the signal thread runs out to the nearby silken retreat. It is abundant throughout Britain and again reaches maturity in late summer or autumn. The female can continue activity until the following spring, the only orb weaver to continue to spin webs through the winter. The female constructs her slightly arched cocoon from dirty-yellow threads, in the corners of houses and the underside of eaves. A dense white web is spun over the cocoon. Sometimes, she may construct two cocoons close together, in which case one web covers both. The cocoons are not camouflaged.

This species was particularly well-represented at Garscube, specimens being found on the holly hedge, a sign post, inside and outside the bicycle shed, on a gate and in the metal framework of a car port. Only one adult male was found (on the car port on 18th October 1989). Adult females were found from the first search on 21st September until 1st November. Juveniles were found and collected in the following spring (1st and 8th June 1990).

LINYPHIIDAE

Subfamily LINYPHIINAE

Bathyphantes sp.

Only the juvenile was found at Garscube, a tiny spider on a large web in the framework of the carport (18th October 1989). The most common species, *B. gracilis* (Blackwall) in Britain is found mature in spring, summer and autumn on its fine sheet web in low vegetation. Furthermore, it overwinters as an adult (Kirchner, 1987), and can have two generations per year. The small, soft white cocoon is placed on the underside of leaves.

Stemonyphantes lineatus (Linnaeus)

A relatively large spider that produces a small sheet web in low vegetation in a wide range of habitats including coastal areas, chalk downland and sandy heathland. It occurs across the whole region and is locally common throughout. Adults can be found in late summer and autumn, and overwinters as an adult (Kirchner 1987).

Two juvenile specimens were collected from dozens on the trunk of a large beech tree. Their webs were strung across the narrow gap between two buttresses. They were collected on May 11th 1990.

Lepthyphantes sp

Only juveniles were found, making identification to species very difficult. *Lepthyphantes* is the largest genus in the subfamily. Adults of several species can be found all year round, and many others are active as adults during the winter. Generally, their simple sheet webs are found in low vegetation, and most are widespread and fairly common.

Four juvenile *Lepthyphantes* were collected, with their sheet webs, from the holly hedge on September 21st 1989.

Linyphia montana (Clerck)

Widespread in Britain, the species is locally common. It is one of the largest spiders in the family, maturing in early summer. The strong, dense, sheet web is found under logs or in bushes, and the spider waits concealed at the edge of the web. The cocoon, placed near the web, is flat and reveals the vivid yellow colour of the eggs within.

A single female specimen was taken from the holly hedge on the 3rd May 1990, though webs of this species were abundant on the hedge throughout spring and early summer.

Linyphia peltata Wider

Even though this species is more common in the south of Britain than the north, its sheet web is still abundant in bushes and the lower foliage of trees. It reaches sexual maturity in early summer after overwintering as a subadult in the upper vegetation (Kirchner 1987).

One specimen was found on an extensive web amongst the lowest, bare, twigs of a yew tree. It was an adult female, found on June 5th.

Microlinyphia impigra (O.Pickard-Cambridge)

This species is found scattered in various localities in Britain, usually in damp areas such as lake-sides and marshes. They mostly mature in early summer, though later in some regions.

An adult female was found on 21st September 1990 on the holly hedge, well away from any water.

Amaurobius fenestralis (Stroem)

The cribellate web of this species is frequently found on the trunks of trees and on outbuildings throughout Britain. They build their webs at night, but will take prey that is trapped in the web at any time. They mature in the autumn. It builds no silken retreat in its shelter under the bark except during the period of egg-laying. The cocoon is a flattened white disc, 6 to 8 mm in diameter, and the female guards it, probably no longer feeding. Eggs are laid in June and July, and the new generation reaches maturity in autumn of the following year, when mating occurs. The adult male probably dies soon afterwards. Thus this species overwinters both as mated adult females, and as juveniles of both sexes.

This was the only cribellate spider found at Garscube, their webs discovered on the bark of various tree species - beech, yew, hawthorn and sycamore. The spider was often very difficult to extract from its hiding place under the bark, even when enticed out using an insect as bait. Therefore more webs were collected than spiders. Adults were found in autumn (mid October to end of November) and juveniles in the following early summer (June 28th).